Appendix A: PDFs of Cited Literature

2nd Corrected AR - 069470

University of Wyoming
Wyoming Scholars Repository

Ecosystem Science and Management Faculty Publications

Ecosystem Science and Management

2014

Livestock grazing and sage-grouse habitat: impacts and opportunities

Chad S. Boyd
Eastern Oregon Agricultural Research Center

Jeffrey L. Beck
University of Wyoming

John A. Tanaka
University of Wyoming, jtanaka@uwyo.edu

Follow this and additional works at: http://repository.uwyo.edu/ecosys_mng_facpub

 Part of the Life Sciences Commons

Publication Information

Boyd, Chad S.; Beck, Jeffrey L.; and Tanaka, John A. (2014). "Livestock grazing and sage-grouse habitat: impacts and opportunities." *Journal of Rangeland Applications* 1, 58-77.

This Article is brought to you for free and open access by the Ecosystem Science and Management at Wyoming Scholars Repository. It has been accepted for inclusion in Ecosystem Science and Management Faculty Publications by an authorized administrator of Wyoming Scholars Repository. For more information, please contact scholcom@uwyo.edu.

JOURNAL OF RANGELAND APPLICATIONS
2nd Corrected AR - 069471
Volume 1, 2014
pp. 58-77
ISSN: 2331-5512

Livestock Grazing and Sage-Grouse Habitat: Impacts and Opportunities

Chad S. Boyd[1], Jeffrey L. Beck[2], and John A. Tanaka[3]

Keywords: *Centrocercus urophasianus*, livestock grazing, mountain big sagebrush, Wyoming big sagebrush, sage-grouse, economics
AGROVOC terms: grouse, sagebrush, livestock, grazing

Abstract

Sage-grouse obtain resources for breeding, summer, and winter life stages from sagebrush communities. Grazing can change the productivity, composition, and structure of herbaceous plants in sagebrush communities, thus directly influencing the productivity of nesting and early brood-rearing habitats. Indirect influences of livestock grazing and ranching on sage-grouse habitat include fencing, watering facilities, treatments to increase livestock forage, and targeted grazing to reduce fine fuels. To illustrate the relative value of sagebrush habitats to sage-grouse on year-round and seasonal bases, we developed state and transition models to conceptualize the interactions between wildfire and grazing in mountain and Wyoming big sagebrush communities. In some sage-grouse habitats, targeted livestock grazing may be useful for reducing fine fuels produced by annual grasses. We provide economic scenarios for ranches that delay spring turnout on public lands to increase herbaceous cover for nesting sage-grouse. Proper rangeland management is critical to reduce potential negative effects of livestock grazing to sage-grouse habitats.

[1] *Chad S. Boyd (chad.boyd@oregonstate.edu ; corresponding author) - Rangeland Ecologist, USDA-ARS, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, OR 97720*

[2] *Jeffrey L. Beck Associate Professor, Wildlife Habitat Restoration Ecology, University of Wyoming, Department of Ecosystem Science and Management, Dept. 3354, 1000 East University Ave., Laramie, WY 82071*

[3] *John A. Tanaka Department Head and Professor, University of Wyoming, Department of Ecosystem Science and Management, Dept. 3354, 1000 East University Ave., Laramie, WY*

Contents

Introduction 60
Overview of Sage-Grouse Habitats 60
Breeding habitat 60
Late brood-rearing/summer habitat 61
Winter habitat 61
Ecology of Sagebrush Plant Communities 62
Impacts of historical livestock grazing and fire 62
Present day sagebrush ecology 62
Present day grazing effects 64
Direct Effects of Livestock Grazing on Sage-Grouse Habitat 64
Indirect Effects of Livestock Grazing On Sage-Grouse Habitat 65
Livestock fencing 65
Livestock water sources 65
Treatments to increase livestock forage 66
Ranching and land fragmentation 67
Do livestock have a role in fuels management? 67
Economics and Sage-Grouse 68
Sage-grouse and ranching 68
Economic efficiency 69
Summary and Knowledge Gaps 70
Acknowledgments 70
Literature Cited 71

Key Points

- *Livestock grazing can directly influence the composition and productivity of herbaceous plants in sagebrush communities; the greatest potential for livestock grazing to affect sage-grouse populations is by influencing nesting or early brood-rearing habitat productivity.*
- *Managed livestock grazing at moderate intensities can be compatible with maintaining sagebrush/bunchgrass plant communities.*
- *Sustained heavy grazing can reduce abundance of perennial grasses and lower suitability of habitat for most seasonal habitat needs of sage-grouse.*
- *Efforts to maximize herbaceous cover in areas frequented by nesting and brooding sage-grouse should be encouraged to increase sage-grouse concealment from nest and chick predators. Livestock grazing should be managed in breeding and brood-rearing habitats to maximize herbaceous growth and maintain functional bunchgrass understories where sagebrush cover exceeds 10%.*
- *Prescription grazing can be used as a tool to decrease continuity, amount, and potentially composition of fine fuels in areas prone to annual grass invasion.*
- *Economic impacts of sage-grouse management practices on ranches vary by both location and degree of change required in livestock management. Changes in season of use, stocking levels, or species grazed will cause changes in the yearlong production cycle of a ranch and differentially affect the economic sustainability of said ranch.*
- *Rangeland altering practices may or may not be economically feasible depending on cost-share arrangements, changes in production practices, or changes in rangeland and animal productivity. Each practice must be analyzed for the specific situation in which it will occur.*

Introduction

Sagebrush ecosystems once covered 1,090,000 km^2 (270,000,000 acres) of the western United States (Beetle, 1960; McArthur & Plummer, 1978) and support widely diverse wildlife species and land use practices. Greater sage-grouse (hereafter, sage-grouse) are a sagebrush obligate wildlife species that inhabits 11 western states and two Canadian provinces and has been experiencing a generalized range-wide decline since at least the 1960s (Connelly et al., 2004). This decline has prompted the US Fish and Wildlife Service to consider listing sage-grouse as a threatened or endangered species under provisions of the Endangered Species Act of 1973 (USFWS, 2010). The sage-grouse decline is associated with widespread loss or modification of sagebrush habitats (Aldridge et al., 2008; USFWS, 2010). These habitats have undergone large scale change in recent decades due to the introduction of exotic annual grass species at low elevations and altered fire regimes with associated expansion of native conifers (Utah, western, and Rocky Mountain Juniper; and piñon pine) at higher elevations (Davies et al., 2011a), as well as large-scale anthropogenic development, particularly in the eastern portion of their distribution (Naugle et al., 2011).

Livestock grazing occurs across much of the sagebrush biome and has the potential to impact both the composition and structure of sage-grouse habitat (Beck & Mitchell, 2000; Crawford et al., 2004). In this paper, we review the ecology of sagebrush habitats, the role of livestock grazing influencing that ecology, and the direct and indirect effects of livestock grazing to habitat quality for sage-grouse. We then develop an economic context for implementing sage-grouse habitat management practices within ranching operations.

Overview of Sage-Grouse Habitats

Breeding habitat

Sage-grouse must select habitats to ensure concealment from predators and to meet biological needs including food acquisition and thermoregulation (Hagen, 2011; Kirol et al., 2012). Breeding habitat for sage-grouse includes strutting

grounds (leks), nesting habitat, and early brood-rearing habitat (Connelly et al., 2000). Conserving intact sagebrush habitat around leks is vital because >90% of nests are aggregated within 10 km (6.2 mi) of leks (Holloran & Anderson, 2005). Female sage-grouse tend to select nesting sites in areas with high cover and height of grasses and sagebrush (Connelly et al., 2000; Hagen et al., 2007), with this selection pattern possibly more pronounced in xeric (i.e., drier) sagebrush systems (receiving less than 25 cm [9.8 in] of precipitation annually; Kirol et al., 2012). Habitat attributes directly around nests and early brood-rearing locations are often very similar because brooding females spend their first two to three weeks after eggs hatch near their nests (Berry & Eng, 1985; Holloran & Anderson, 2005). The availability of insects, particularly ants and beetles, is a critical component of early brood-rearing habitat quality because sage-grouse chicks require high protein foods (i.e., insects and actively growing forbs) almost exclusively for the first two weeks after hatching (Peterson, 1970; Johnson & Boyce, 1990). Grasshoppers also form an increasingly important insect food for chick sage-grouse during late brood-rearing (Klebenow & Gray, 1968). Before nesting, sage-grouse hens also likely select habitats where they can obtain a higher nutritional status for reproduction (Barnett & Crawford, 1994; Gregg et al., 2008). Generally, breeding habitats are characterized by a well-developed sagebrush overstory and an abundant understory of herbaceous plants (Connelly et al., 2000). In sage-grouse breeding habitat, livestock grazing is of interest because of its potential effects on insect and forb abundance, shrub cover, and the herbaceous understory.

Late brood-rearing/summer habitat

As summer progresses, chick sage-grouse consume fewer insects and more forbs (Klebenow & Gray, 1968; Peterson, 1970). Consequently, late brood-rearing habitat is typically associated with mesic sites that produce forbs and insects eaten by hens and chicks (Schroeder et al., 1999; Connelly et al., 2000). There is a tendency for birds to move to more mesic sagebrush communities at higher elevation or to find sagebrush stands adjacent to wetlands, seeps, or riparian environments where forbs are more prominent (Fischer et al., 1996b). However, sage-grouse in drier sagebrush communities may still exhibit a close association with sagebrush and grass during the late brood-rearing period (Kirol et al., 2012).

Winter habitat

Sage-grouse use forbs in autumn until they senesce and become unavailable. At this time, grouse shift to feeding on sagebrush leaves and consume, almost exclusively, sagebrush throughout the winter (Wallestad & Eng, 1975). Thus, winter habitats must provide sagebrush that is tall enough to project above snow levels so grouse can forage. In general, wintering sage-grouse tend to select flatter topography in areas with large contiguous patches of dense sagebrush (Eng & Schadweiler, 1972; Doherty et al., 2008; Carpenter et al., 2010). Remington and Braun (1988) documented that all age and sex classes of sage-grouse wintering in North Park, Colorado gained or maintained weight and fat over winter. They concluded that the limited energy reserves that sage-grouse acquire are probably most important for breeding and nesting, not winter survival (Remington & Braun, 1988). In winter, sage-grouse may form flocks of only males or females, and restrict habitat use to small areas within the landscape (Beck, 1977). Sage-grouse are noted for their preference for sagebrush species or sub-species and individual plants in winter that are more palatable or nutritious. For example, Remington and Braun (1985) reported that sage-grouse in north-central Colorado selected individual big sagebrush plants having higher crude protein levels than random or unbrowsed plants. In an enclosed, uniform sagebrush garden in Utah stocked with six wild-caught birds, Welch et al. (1991) observed winter foraging preference for three subspecies and nine accessions of big sagebrush collected at various sites in Utah. These authors reported the order of foraging preference was mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush (Welch et al., 1991). Recently, sage-grouse were shown to make multi-hierarchical decisions in habitat selection by first selecting black sagebrush sites, which had lower plant secondary metabolites than Wyoming big sagebrush sites, then selecting patches and individual black sagebrush plants within those patches that had lower plant secondary metabolites and higher crude protein (Frye et al., 2013). It is therefore important to understand how grazing may influence the structure and

chemical composition of individual plants and the sagebrush species composition on a site.

Ecology of Sagebrush Plant Communities

Impacts of historical livestock grazing and fire

Fire and herbivory are dominant disturbance factors influencing plant communities across the sagebrush biome. However, changes in grazing practices and fire regimes make it important to differentiate between the historic and present day impacts of these disturbances. European settlement and development of a livestock industry initiated dramatic changes in spatial and temporal patterns of grazing within sagebrush communities (Miller et al., 1994). Long periods of livestock use combined with high stocking rates resulted in decreased perennial grass and increased shrub abundance (Mack, 1981; Young & Sparks, 1985). At low elevations typified by Wyoming big sagebrush and low sagebrush, diminished perennial herbaceous vegetation and high levels of ground disturbance promoted the establishment of exotic annual grass species such as cheatgrass (Mack, 1981). Before the arrival of exotic annual grass species in the late 1800s, mean fire return interval (MFRI) in low elevation sagebrush steppe communities has been estimated at 50 to 100 years (Wright & Bailey, 1982). In higher elevation communities typified by mountain big sagebrush MFRI prior to European arrival was 12 to 25 years on mesic sites and up to 200 years on drier sites (Crawford et al., 2004). High livestock stocking rates likely reduced fine fuels and decreased fire frequency, resulting in expansion of fire-sensitive native conifer populations into areas previously dominated by sagebrush/bunchgrass plant communities at higher elevations (Riegel et al., 2006).

Present day sagebrush ecology

Present day ecology and successional drivers of sagebrush plant community dynamics differ markedly along an elevation gradient. At low elevations, these communities can shift from co-dominance by shrubs with an understory of perennial grasses and forbs to grass-, shrub-, or annual grass-dominated plant communities (Davies et al., 2011b; Figure 1). Fire, even of low severity, can dramatically reduce sagebrush abundance because both big and low sagebrush plants are killed by fire and do not resprout following fire. Perennial grasses often recover from low severity fire, but may be killed under high severity fire, leading to dominance of the post-burn community by annual grasses (Miller & Eddleman, 2001).

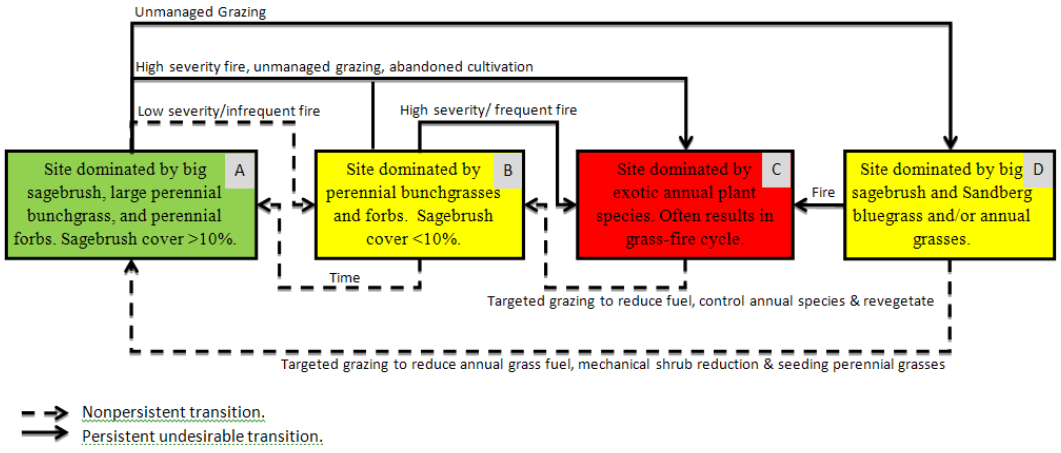


Figure 1. Successional model depicting present-day vegetation states and causes of transition between these states for low to mid-elevation sagebrush plant communities. This model generalizes characteristics for sites dominated by Wyoming big sagebrush. The green box denotes vegetation capable of providing year-around habitat for sage-grouse. Yellow boxes denote potential seasonal habitat and the red box indicates non-habitat. Targeted grazing to reduce annual grass fuel loading in states C or D may have indirect positive impacts at larger scales by reducing fire spread to intact plant communities (states A or B). Use of targeted grazing in state D should focus on reducing annual grass fuels to minimize probability of fire and subsequent transition to state C. Figure adapted from Crawford et al. (2004).

Moderate levels of grazing generally do not cause major shifts in relative abundance of plant functional groups (Miller et al., 1994), but sustained heavy grazing can reduce perennial bunchgrasses and promote sagebrush dominance with an annual grass understory (Strand et al., 2014). Defining specific levels of grazing that constitute moderate or heavy grazing is difficult because the effects of herbivory on plants vary strongly by species, site conditions, season, and year (Caldwell, 1984; Westoby, 1989; Crawford et al., 2004). Once annual grasses become dominant, wildland fire tends to become more frequent, which further promotes dominance of annual grasses (Miller et al. 1994). The continuous fine fuel bed created by annual grasses promotes easier ignition and MFRI can decrease to <10 years (Whisenant, 1990). Native perennial species are not adapted to frequent fire and are dramatically reduced or eliminated from the plant community. Exotic annual grasses now occupy or threaten to invade over 30 million hectares (74 million acres) of sagebrush rangelands (Meinke et al., 2009). These species promote large, frequent wildfires, reduce livestock forage quality, decrease biodiversity (D'Antonio & Vitousek, 1992; Davies, 2011) and reduce the quality of or eliminate habitat for sagebrush obligate wildlife species (Crawford et al., 2004).

At mid- to high-elevation, sagebrush plant community composition historically fluctuated in a fire-driven cycle between co-dominance by sagebrush, perennial grasses and forbs, and post-fire grass/forb communities (Figure 2). Sagebrush is reduced or eliminated by fire, but returns via post-fire regeneration from seed (Ziegenhagen & Miller, 2009). Compared to lower elevations, perennial grasses and forbs at these higher sites generally recover more quickly from fire, and sagebrush is more likely to reestablish after fire (Miller & Eddleman, 2001). Reduced fire frequency at mid to high elevations has been further accentuated by improvements in firefighting techniques and the availability of mechanized equiptment (Pyne et al., 1996).

However, in the relative absence of fire, native conifers (which are easily killed by fire) have expanded to occupy nearly 19 million hectares (47 million acres) in the Intermountain West (Miller & Tausch, 2001; Miller et al., 2005; Davies et al., 2011b), leading to loss of understory perennial species, dramatically increased soil erosion, and loss of critical wildlife habitat (Bates et al., 2000; Miller et al., 2005; Pierson et al., 2007). The majority of the area of conifer expansion is within the range of sage-grouse (Crawford et al., 2004).The specific effects of conifer expansion on understory shrub and herbaceous plant communities depend on soil conditions. On sites with limiting soil layers not far below the surface, both shrubs and

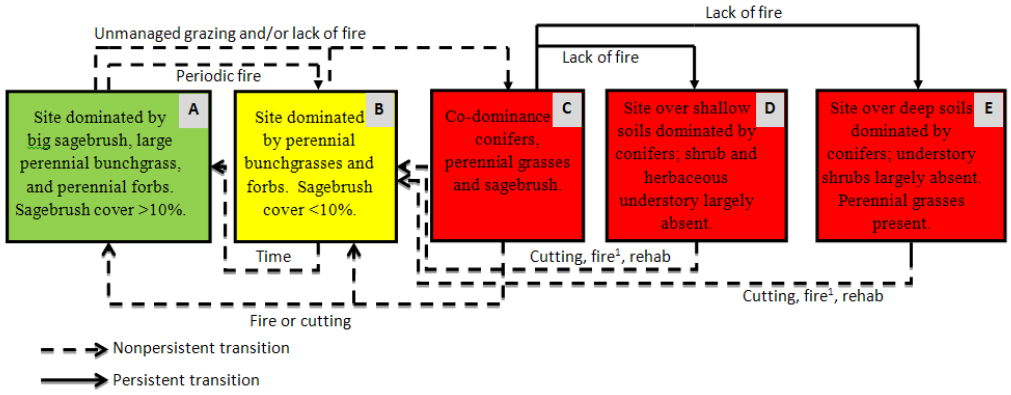


Figure 2. Successional model depicting present-day vegetation states and causes of transition between these states for mid to high elevation mesic sagebrush plant communities. This model generalizes characteristics for mountain big sagebrush. The green box denotes vegetation capable of providing year-around habitat for sage-grouse. The yellow box denotes potential seasonal habitat and red boxes indicate non-habitat. Figure adapted from Miller et al. (2005).

[1] Burning opportunities in states D and E may be limited if fine fuels have been substantially reduced by juniper competition. In such cases, post-juniper removal rehabilitation may be necessary to restore understory herbaceous and woody plant diversity.

herbaceous plants are generally lost as conifer abundance approaches stand closure (Miller et al., 2005). On sites with deeper soils, herbaceous plants can be retained, even at high levels of conifer abundance, but shrubs are generally lost over time.

Present day grazing effects

There are several ways that modern livestock grazing can influence sagebrush ecosystems and sage-grouse habitat. Figures 1 and 2 depict generalized dominant vegetation transitions that apply broadly across the range of sage-grouse; they do not include conditions in all sagebrush community types. Within these figures, the effects of livestock grazing on plant community composition and structure vary with timing and intensity of grazing. The herbaceous understory of sagebrush plant communities is comprised largely of cool season bunchgrasses that are sensitive to grazing during peak growth periods (late spring and early summer). Heavy or repeated grazing during this period can decrease vigor and production of perennial bunchgrasses and forbs, and may cause compositional shifts toward increased shrub abundance over time (Mueggler, 1950; Laycock, 1967; Bork et al., 1998; Ganskopp et al., 2004). Prescribed spring or fall grazing can be used as a tool to reduce the seed pool and biomass of exotic annual grasses (Diamond et al., 2012; Schmelzer et al., In Press). However, timing should focus on either early spring when annuals are photosynthetically active and perennial bunchgrasses have not yet broken dormancy (Smith et al., 2012), or after perennial grasses' dormancy in fall. If grazing by cattle occurs after grass flowering, preference can shift from grasses to shrubs, leading to reduced shrub abundance over time (Ganskopp et al., 1999). The effects of prolonged heavy livestock grazing are most often observed as decreased perennial bunchgrasses, increased shrub abundance, and, at lower elevations, potential increases in annual grass abundance (West, 1989; Miller et al., 1994; Schuman et al., 1999). The effects of light to moderate utilization are more difficult to predict because of the more subtle nature of these effects. The balance of available evidence suggests that light to moderate livestock use (up to approximately 50% of available yearly perennial grass biomass) can be compatible with maintenance of perennial vegetation (Sneva et al., 1984; Miller et al,. 1994), but the net impact of different use levels will vary strongly in accordance with climatic variability, local environment, and season of use (Westoby et al., 1989; Crawford et al., 2004).

Direct Effects of Livestock Grazing on Sage-Grouse Habitat

There are no studies that directly test effects of livestock grazing on sage-grouse habitat. However, livestock grazing directly influences the composition, productivity, and structure of herbaceous plants in sagebrush plant communities; thus the greatest direct effect livestock grazing likely has on sage-grouse populations is influence on the productivity of nesting or early brood-rearing habitats (Beck & Mitchell, 2000; Hockett, 2002; Cagney et al., 2010). Sagebrush browsing by domestic sheep and goats, or impacts from sheep bed grounds, could also negatively influence sage-grouse in winter by reducing cover and height of sagebrush stands used by sage-grouse (Rasmussen & Griner, 1938). Nest selection in Wyoming was predicted to occur in areas with increased total shrub canopy cover and residual (i.e., last year's growth) grass cover and increased height compared to random sites; furthermore, successful nests compared to unsuccessful nests were best predicted by residual grass cover and height (Holloran et al., 2005). Similarly, chick survival has also been predicted by grass cover at the microhabitat scale (Gregg & Crawford, 2009). The effects of grazing on nesting habitat may be complicated by grazing preferences at small scales. For example, research has shown that cattle prefer to graze grasses in openings between shrubs over those under shrub canopies (where sage-grouse would most likely nest), but preference for undercanopy plants increases if grass utilization at the pasture scale exceeds 40% by weight (France et al., 2008).

The intensity and timing of livestock grazing can modify plant communities and may directly influence sage-grouse nest selection and nest and chick survival. Managing livestock grazing to maintain adequate residual grass height and cover under shrubs in spring is likely to minimize effects of grazing on sage-grouse productivity. In general, efforts to increase residual herbaceous cover following grazing in areas frequented by nesting and brooding sage-grouse should enhance concealment from nest and

chick predators. In addition, it is important to manage grazing in a way that maximizes current-year herbaceous growth in breeding habitats which include sagebrush cover exceeding 10% and which have functional bunchgrass understories, given the high value of such sites to nesting and brood-rearing sage-grouse (Connelly et al., 2000; Cagney et al., 2010*)*. Grazing may bring some positive benefits to other attributes of sage-grouse habitat. For example, some evidence suggests that moderate cattle grazing in mesic meadows frequented by sage-grouse may expose forbs selected by sage-grouse (Neel, 1980; Klebenow, 1982; Evans, 1986).

Indirect Effects of Livestock Grazing On Sage-Grouse Habitat

Livestock fencing

Sage-grouse collide with and are killed by linear manmade features, including power lines (Beck et al., 2006) and fences (Stevens et al., 2012a, Stevens et al., 2012b). Stevens et al. (2012a) studied sage-grouse fence collisions associated with breeding habitats in southern Idaho. They reported that fence collisions may be influenced by fence segments without wooden fence posts and/or where fence segments exceed 4 m (13.1 feet). Results from this study suggested fence modification in sage-grouse breeding habitats should target areas with fence densities exceeding 1 km/km^2 (0.62 mile/mile^2) within 2 km (1.2 miles) of active leks in areas with flat to gently rolling terrain. Furthermore, site-scale modeling results suggested constructing fences with larger and more conspicuous wooden fence posts and segment widths less than 4 m (13 feet) to reduce fence collisions (Stevens et al., 2012a). In addition, marking fences may reduce risk of fence collision by as much as 83% (Stevens et al, 2012b).

Livestock water sources

Livestock watering developments primarily affect sage-grouse habitat through their influence on livestock distribution and subsequent patterns of grazing intensity (i.e., utilization levels) in pastures. In arid regions, where natural water is limited, water plays the primary role in determining distribution of grazing livestock (Ganskopp, 2001). Salt, mineral, and nutrient supplements have been reported to alter livestock distribution in a manner similar to water placement (Ares, 1953). However, this effect is not consistent across studies, and when both salt/mineral and water placement have been simultaneously evaluated, water is by far the dominant factor influencing livestock distribution (Bailey & Welling, 1999; Ganskopp, 2001). Water sources located near breeding habitat may cause intensive livestock grazing that can limit herbaceous screening cover at nest locations, which could potentially increase nest predation (Gregg et al., 1994; Sveum et al., 1998). In addition, livestock water developments are spatially extensive and have increased the amount of sage-grouse habitat that is grazed (Connelly et al., 2004). Furthermore, artificial water developments can be used to attract and re-distribute grazing livestock to non-critical habitat (Ganskopp, 2001).

Sage-grouse do not require standing water (Schroeder et al., 1999; Connelly et al., 2000), but they will use it where available (Dalke et al., 1963). They are not, however, particularly adept at negotiating standing water, so water developments have the potential to impact sage-grouse mortality both directly and indirectly. Direct mortality has been reported through drowning in stock tanks; the range-wide impact of these mortalities is unknown, but limited data suggest that drowning mortality can be substantial at local scales (e.g., Sika, 2006). To reduce incidence of drowning, escape ramps should be installed in stock tanks (Connelly et al., 2000).

Indirect sage-grouse mortality from livestock water developments is associated with disease. West Nile Virus is carried by the encephalitis mosquito that reproduces in standing water, including livestock water developments (Connelly et al., 2004). These insects then transmit the disease to sage-grouse and other avian species (Naugle et al., 2004). Survival rates for infected sage-grouse are very low (Clark et al., 2006) and impacts have been measured at the population scale (Naugle et al., 2005; Taylor et al. 2013).

The net effect of water developments on sage-grouse is complicated by the fact that they also may provide food resources for sage-grouse in the form of mesic vegetation (Wallestad, 1971). Locating livestock water

developments within sage-grouse summer (i.e., late brood rearing) habitat will decrease impacts to winter and breeding habitat and provide a potentially usable source of both water and succulent plants during the driest portion of the year (Connelly et al., 2000). However, these benefits must be weighed against the potential for increased incidence of mosquitoes carrying West Nile Virus. Limiting the number and size of new livestock water sources and/or turning water off in tanks after livestock have been moved from pastures should be considered to reduce standing water used by mosquitos that are vectors for West Nile virus (Walker & Naugle, 2011).

Treatments to increase livestock forage

Prescribed fire is a tool that can be used to promote livestock forage abundance; however, because fire kills sagebrush and sage-grouse are sagebrush obligates, its potential application must be carefully evaluated. At lower elevations many studies indicate little benefit of fire to food or structural habitat resources for sage-grouse (Fischer et al., 1996a; Beck et al., 2009; Rhodes et al., 2010; Bates et al., 2011; Beck et al., 2012; Hess & Beck, 2012). Risk of post-fire transition to annual grass dominance (Figure 1), combined with lack of substantive benefit to habitat elements important to sage-grouse suggests extreme caution when using prescribed fire in low-to-mid elevations (Chambers et al. 2013). Conducting burns in Wyoming big sagebrush communities is strongly discouraged because annual grasses often increase and perennial vegetation cover and structure required by sage-grouse either do not recover or recover very slowly after burning (Beck et al., 2009; Beck et al., 2012; Hess & Beck, 2012). One exception to this generalization would be the use of prescribed fire to reduce ground cover prior to treatment with soil active herbicides for controlling annual grasses within annual grass monocultures (e.g., Davies & Sheley, 2011).

In mid- to high-elevation mesic habitats where mountain big sagebrush dominates, the effects of fire on sage-grouse habitat are largely contingent on fire size and/or frequency. Small prescribed burns within a larger mountain big sagebrush landscape have been used as a technique to increase herbaceous plant production and improve brood-rearing habitat (e.g., Thacker, 2010). Alternatively, larger fires that kill sagebrush across vast areas can severely reduce habitat availability: such treatments should be avoided (Boyd et al., 2011; Beck et al., 2012). When longer time periods are considered, fire may be needed to prevent conifer expansion (Figure 2) and associated loss of sage-grouse habitat quality (Miller & Eddleman, 2001). However, the immediate loss of sagebrush (for perhaps several decades) with fire can decrease habitat quality, which underscores the importance of considering spatial scale when using prescribed fire as a management tool in mountain big sagebrush communities.

Mechanical and herbicide-based reduction of sagebrush have been used on millions of hectares in the western United States as management techniques to increase production of herbaceous livestock forage species (Beck & Mitchell, 2000; Crawford et al., 2004). At higher elevations, some evidence suggests that mechanical reduction can enhance grass and forb production in sage-grouse brood-rearing habitat (Dahlgren et al., 2006). At lower elevations, mechanical sagebrush reduction has had either indeterminate or negative consequences (mainly long-term reduction in sagebrush abundance) and is not recommended where sage-grouse habitat is present (Davies et al., 2009a; Davies et al., 2011a; Hess & Beck, 2012). Herbicide-based control of sagebrush initially centered on maximum shrub kill using 2,4-D; although herbaceous production often increased dramatically post-treatment, concerns over loss of herbaceous diversity (particularly forbs) have limited use of 2,4-D on rangelands (Crawford et al., 2004; Beck et al., 2012). Subsequent work with low rate application of Tebuthiuron indicates a potential to reduce, but not eliminate sagebrush cover while increasing production of grasses and forbs, which could have positive impact on sage-grouse food resources (Olson et al., 1994; Olson & Whitson, 2002; Dahlgren et al., 2006). Large scale sagebrush reduction is not desirable, particularly within winter or nesting habitat (Dahlgren et al. 2006; Beck et al., 2012).

Another indirect effect of livestock grazing on sage-grouse habitat is the planting of exotic perennial species to provide livestock forage. This practice has often been accompanied by removal of competing vegetation such as sagebrush, and forage species such as crested wheatgrass and affiliates are largely planted in monoculture. The major impact of such

conversions on sage-grouse is removal of the shrub component, and the potentially reduced availability of forbs due to competition with seeded grasses; without sagebrush, year-round habitat for sage-grouse and other sagebrush obligates is eliminated (Reynolds & Trost, 1981; McAdoo et al., 1989). Consequences of monoculture plantings on specific sage-grouse populations also relate to the scale of planting, and the availability of alternate habitat resources. Less clear is the impact of non-native perennials occurring in mixed stands with an intact sagebrush component. In other ecosystems, avian diversity has not suffered with increases in non-native perennial species as long as key habitat structural components are maintained (Davis & Duncan, 1999; Kennedy et al., 2009). Similar research in sagebrush systems suggests that crested wheatgrass seedings without a sagebrush component provide poor habitat structure for sagebrush obligate bird species (Reynolds & Trost, 1980). However, avian species diversity may increase as crested wheatgrass monocultures are re-colonized by shrubs and as structural complexity of the habitat is re-established (McAdoo et al., 1989).

One complicating factor in evaluating the long-term impacts of non-native perennials on sage-grouse habitat is the use of these species within a rehabilitation context (e.g., post-fire seeding), particularly at low- to mid-elevations where the success of establishing crested wheatgrass can be orders of magnitude higher than that of native perennials (Davies et al., 2011b; Boyd & Davies, 2012a; Boyd & Davies, 2012b). Perennial bunchgrasses are important to curtail the spread and dominance of exotic annual grasses. Perennial bunchgrasses are poor competitors with annual grasses at the seedling stage, but, when mature, can effectively occupy a site and prevent further expression of annual species (Chambers et al., 2007; Young & Mangold, 2008). Thus, in some instances, crested wheatgrass can be a valuable resource in helping to prevent the spread of exotic annual grasses, and this value should be factored into determinations of long term impact on sage-grouse habitat. One potential drawback to the use of crested wheatgrass in the restoration context is that it is exceptionally difficult to re-introduce native species in established crested wheatgrass communities due to the competitive nature of this non-native perennial (Rafferty & Young, 2002; Monaco et al., 2005). However, recent evidence suggests that establishing sagebrush transplants within crested wheatgrass communities can be successful, at least at small scales (McAdoo et al., 2013). Research also indicates that prescribed grazing of perennial grasses by livestock can help to promote restoration of sagebrush and other shrubs in grass-dominated plant communities (Austin et al., 1994; Ganskopp et al., 2004).

Ranching and land fragmentation

It is widely accepted that sage-grouse benefit from expansive unfragmented landscapes. However, there are few research studies providing evidence that the continued existence of traditional ranches prevents land fragmentation or conversion to other uses such as subdivisions, rather than for livestock grazing. Recent research (Gosnell & Travis, 2005) suggests that there is a trend towards “amenity” ranches in the Rocky Mountain region. The implication is that recent ranch purchases are being made by absentee owners seeking to own the open space of the West. Torell et al. (2005) found that ranch sales prices in New Mexico were more influenced by amenity and lifestyle values than income potential. Similar results were found for ranches in the Great Basin (Rimbey et al., 2007). In the Great Basin, ranches were purchased for expected investment appreciation, recreation and lifestyle opportunities, and prestige. While it is fairly well established that ranches are bought and sold based more on amenity and lifestyle values than traditional ranching, it is not clear whether this motivation is enough to prevent subdividing large tracts of private land. It is known that there are the amenity and lifestyle motivations to keeping large tracts intact. The decision to subdivide will depend on the motivation of the current landowner and the relative values they place on income from land sales versus the amenity, lifestyle, and ranching income derived from the intact ranch.

Do livestock have a role in fuels management?

At low to mid-elevations in the Great Basin and Colorado Plateau, wildfire frequency and size have increased dramatically in recent years, due in part to

the continuous fuel bed associated with annual grass communities (NIFC, 2012). These large fires, and the difficulties associated with post-fire restoration at lower elevations, present serious challenges to sage-grouse habitat restoration. For example, in southeast Oregon, over 404,700 hectares (1 million acres) of sagebrush habitat (nearly 10% of the sage-grouse core habitat in the state) burned in the 2012 fire season in three large wildfires (NIFC, 2012). With these challenges in mind, livestock grazing could have a role in altering fuel characteristics either to reduce probability of wildfire ignition, to increase effectiveness of suppression techniques, or both (Strand et al., 2014). To date, there have been few empirical efforts to document the effects of livestock grazing on fire ignition or behavior. One study (Diamond et al., 2009) reported that heavy grazing of annual grasses during spring reduced probability of ignition, flame length, and rate of spread. Additional research is needed to determine if the effects of livestock grazing can sufficiently alter fuel loading and fire characteristics (e.g., maximum temperature and duration of temperature) to reduce fire-induced mortality of herbaceous perennial plant species important to sage-grouse (Wright, 1970). Davies et al. (2009b) reported that long-term rest from grazing amplified perennial grass mortality during fire as compared to long-term grazing at moderate levels. Non-grazed areas in this study had increased accumulation of dead herbaceous fuels and experienced significant annual grass invasion post-fire (Davies et al., 2010).

Economics and Sage-Grouse

Rangeland treatments and management practices have been evaluated in a variety of settings. Yet, there is very little published research on the economics of managing sage-grouse habitat. This is likely because there is no market-based value for sage-grouse; once the decision is made to treat their habitat, the best that can be done is to examine the alternatives and find the lowest cost alternative. The least cost alternative is rarely the most economically efficient or optimal alternative (i.e., the highest net return for society); it is only the least cost way to achieve an already decided upon management objective. For example, deciding to manage sagebrush density with a particular treatment may use a least cost method (e.g., chemicals versus mechanical) rather than determining if doing that treatment leads to the most profitable use of those funds. With that in mind, we will examine what is known about economics related to sage-grouse management. Specific information on economic analysis is presented in Torell et al., (2002) and Torell et al., (2014).

Sage-grouse and ranching

Given that the primary identified change in ranching is likely going to be a change in early spring grazing to increase herbaceous nesting cover, several authors completed a study of the impacts of delaying turn-out of cattle (i.e., eliminating the early spring grazing season) or reducing federal grazing land allotments for typical ranches in Oregon, Idaho, and Nevada (Torell et al., 2002). The models assumed that cattle turn-out onto Bureau of Land Management (BLM) lands would be delayed by one month and that the only alternatives the ranch had were to either extend the hay feeding period or reduce the herd size, depending on which was most profitable (Table 1).

The representative ranches in Nevada and Idaho responded similarly by reducing herd size and with reductions in total BLM Animal Unit Months (AUMs) used. In those cases, the loss of early spring forage resulted in less overall use of the remainder of the BLM permit. In other words, early spring use was the limiting season and the model adjusted herd size based on that resulting in less forage and feed demand yearlong. The Oregon model did not exhibit that response and shifted the BLM AUM use to later in the year and adjusted other forage and feed sources. In Oregon, the response was to increase herd size even though the ranch made less profit. In Nevada and Idaho, herd size was reduced and profits were lower. It was estimated that the annual average economic loss from the loss of the early spring BLM permit was $3/AUM in Idaho, $6/AUM in Nevada, and $10/AUM in Oregon. These results depend on cattle prices and input costs (especially hay) that existed at that time.

The Oregon model appears to be an anomaly. The Oregon model appears to have more flexibility in

Table 1. Results from no early spring (No Spring) grazing in BLM allotments in representative ranches in northeastern Nevada, southwestern Idaho, and south central Oregon, compared to the baseline ranch with early BLM spring grazing.

	Nevada		Idaho		Oregon	
	Base	No Spring	Base	No Spring	Base	No Spring
Herd Size (AUY)	728	589	345	274	723	742
Brood Cows	419	341	223	175	416	425
Annual Net Cash Income	30,795	13,624	8,856	2,862	50,059	44,452
Probability of negative net annual cash income (%)	25	37	35	45	16	19
BLM AUMs used	3,871	2,187	1,655	972	2,400	2,400

using hay than in the other two. It was still more profitable to redistribute grazing on BLM and private lands and to feed more hay than it was to reduce herd size. The results that they make less money doing this explain why the model does not allocate forage in this way, even without the sage-grouse restriction. The higher loss per AUM is explained similarly. Even though this ranch will have higher cattle sales, the added costs of hay more than offset that gain. In the case of Idaho and Nevada, with smaller herd sizes, the ranches are able to sell some of their own produced hay to offset the lower cattle sales. These scenarios demonstrate the variability in responses of individual ranches to the same management change.

Economic efficiency

Earlier in this paper, some changes in infrastructure were suggested which could modify sage-grouse habitat (i.e., changes in livestock fencing, watering sources, forage resources, and using livestock for fuels treatments). Each of these alternatives must be analyzed for its effect on economic efficiency. The methods used for this are described by Torell et al. (2014). The analysis of each change depends on the expected change in benefits and changes in costs, the timing of those changes, and the discount rate used. Because the changes are being made to benefit sage-grouse, a wildlife species with an unknown value to society, a true economic evaluation is not possible. In this case, finding least-cost alternatives that will have the greatest benefit to the species is where limited investment funds should be put. For example, if standard livestock fencing of metal T-posts and barbed wire is found to have the greatest impact on bird mortality, the recommendation to replace that fencing with wooden posts could be analyzed by funding the costs of removing the T-posts and installing wooden posts. If, however, wildfires are found to have the greatest impact on bird populations, then those limited funds should be invested in the least-cost alternatives to reduce fire risk.

Risk of bird mortality from each alternative infrastructure change should also be part of the evaluation. While large-scale wildfires would be expected to have significant short- and long-term effects on bird populations, the risk of a wildfire occurring in any given location may be low. On the other hand, if a fence is left in place there may be a low probability of a bird hitting it, but a relatively high probability of mortality if it does. If those probabilities were known in each case, better investment decisions could be made. At present, it is more likely that professional estimates drive these kinds of decisions rather than research-based measurements.

From a societal standpoint, limited investment funds should be put where they will have the greatest return on investment (Workman, 1986; Tanaka & Workman, 1990). In general, that will mean either maintaining or improving conditions in the best habitat. Investments in areas that are marginal habitat will not result in very significant returns and are by definition not good economic investments. Alternatively, there may be spatial linkages between poor and excellent habitat that impact this generality. For example, high probability of ignition in annual grass communities near excellent habitat suggests that maintaining the excellent habitat could involve fuels treatment in

non-habitat (i.e., annual grass) areas. It is very important to note that when economic analyses of rangeland improvement practices have been done as part of ecological or livestock management research studies, it is rare to find ones that have positive economic returns when livestock production is the sole benefit (Tanaka et al., 2011). In these cases, consideration of the (largely unknown) economic values for other ecosystem services may be what makes these decisions economically feasible.

Summary and Knowledge Gaps

To provide cover for nests and chicks, livestock grazing should be managed in breeding habitat to promote residual cover for concealing sage-grouse nests and chicks from predators. Consequently, research on grazing parameters that promote nest and chick survival for sage-grouse populations (including timing, class of livestock, and duration and intensity of use) is needed. Ranch and rangeland managers can reduce the indirect influences of grazing practices by following recommendations to reduce fence collisions, limiting livestock watering facilities and turning them off when not in use, by installing bird ramps in stock tanks, and by avoiding treatments that reduce long-term sagebrush abundance. Understanding how livestock grazing impacts the structure and composition of sagebrush plant communities provides a critical foundation for assessing the ramifications of grazing to sage-grouse habitat. Establishing a common understanding can reduce conflict over grazing management and focus management efforts in the most impactful direction.

Additional research is needed to more clearly define the role of grazing as a fuels management tool to reduce severity of wildfires. Basic research is also needed to supplement our knowledge of long-term (i.e., multi-decade) impacts of moderate levels of grazing on structure and composition of sagebrush habitats and how these impacts interact with dominant environmental gradients such as precipitation. Research to understand the economic impact of management changes to treat sage-grouse habitat on public and private land needs to be developed at least on a regional basis. Research is also needed to understand the impact of any change in management or implementation of a management practice on bird populations. In economic terms, the development of a production function with associated probabilities of occurrence is needed to better model economic impacts.

Acknowledgments

This manuscript was requested and supported by the Owyhee Initiative (www.owyheeinitiative.org/). The work of these authors was also supported by the USDA National Institute of Food and Agriculture, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center; and the University of Wyoming, Department of Ecosystem Science and Management. USDA and the University of Wyoming are equal opportunity providers and employers.

Common and Scientific Names of Plants Listed in Text According to the USDA PLANTS Database (for plants only; www.plants.usda.gov/).

Common Name	Scientific Name
Black sagebrush	*Artemisia nova* A. Nelson
Basin big sagebrush	*Artemisia tridentata* Nutt. ssp. *tridentata*
Cheatgrass	*Bromus tectorum* L.
Crested cheatgrass	*Agropyron cristatum* (L.) Gaertn.
Little sagebrush	*Artemisia arbuscula Nutt.*
Piñon pine	*Pinus monophylla* Torr. & Fren, *Pinus edulis* Engelm.
Rocky Mountain juniper	*Juniperus scopulorum* Sarge.
Utah juniper	*Juniperus osteosperma* (Torr.) Little
Western juniper	*Juniperus occidentalis* Hook.
Wyoming big sagebrush	*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young
Mountain big sagebrush	*Artemisia tridentata* Nutt. *spp. vaseyana* (Rydb.) Beetle

Common and Scientific Names of Animals Listed in Text According to the Integrated Taxonomic Information System (www.itis.gov).

Common Name	Scientific Name
Cattle	*Bos taurus*
Encephalitis mosquito	*Culex tarsalis*
Goat	*Capra hircus*
Greater sage grouse	*Centrocercus urophasianus*
Sheep	*Ovis aries*

Literature Cited

Aldridge, C. L., Nielsen, S. E., Beyer, H. L., Boyce, M. S., Connelly, J. W., Knick, S. T., & Schroeder, M. A. (2008). Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions, 14*(6), 983-994. doi:10.1111/j.1472-4642.2008.00502.x

Ares, F. N. (1953). Better cattle distribution through the use of meal-salt mix. *Journal of Range Management*, *6*(5), 341-346. doi:10.2307/3894319

Austin, D. D., Urness, P. J., & Durham, S. L. (1994). Impacts of mule deer and horse grazing on transplanted shrubs for revegetation. *Journal of Range Management, 47*(1), 8-11. doi:10.2307/4002832

Bailey, D. W., & Welling, G. R. (1999). Modification of cattle grazing distribution with dehydrated molasses supplement. *Journal of Range Management*, *52*(6), 575-582. doi:10.2307/4003626

Barnett, J. K., & Crawford, J. A. (1994). Pre-laying nutrition of sage-grouse hens in Oregon. *Journal of Range Management*, *47*(2), 114-118. doi:10.2307/4002817

Bates, J. D., Miller, R. F., & Svejcar, T. J. (2000). Understory dynamics in cut and uncut western juniper woodlands. *Journal of Range Management*, *53*(1), 119-126. doi:10.2307/4003402

Bates, J. D., Rhodes, E. C., & Davies, K. (2011). Impacts of fire of sage-grouse habitat and diet resources. *Natural Resources and Environmental Issues*, *17*(1), Article 15, 1-17. Retrieved from http://digitalcommons.usu.edu/nrei/vol17/iss1/15/

Beck, J. L., & Mitchell, D. L. (2000). Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin*, *28*(4), 993-1002.

Beck, J. L., Reese, K. P., Connelly, J. W., & Lucia, M. B. (2006). Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin*,

34(4), 1070-1078. doi:10.2193/0091-7648(2006)34[1070:MASOJG]2.0.CO;2

Beck, J. L., Connelly, J. W., & Reese, K. P. (2009). Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. *Restoration Ecology*, *17*(3), 393-403. doi:10.1111/j.1526-100X.2008.00380.x

Beck, J. L., Connelly, J. W., & Wambolt, C. L. (2012). Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. *Journal of Rangeland Management*, *65*(5), 444-455. doi:10.2111/REM-D-10-00123.1

Beck, T. D. (1977). Sage grouse flock characteristics and habitat selection in winter. *The Journal of Wildlife Management*, *41*(1), 18-26. doi:10.2307/3800086

Beetle, A. A. (1960). *A study of sagebrush. The section Tridentatae of Artemisia* (Bulletin No 368). Laramie, WY, USA: University of Wyoming, Wyoming Agricultural Experiment Station.

Berry, J. D., & Eng, R. L. (1985). Interseasonal movements and fidelity to seasonal use areas by female sage grouse. *The Journal of Wildlife Management*, *49*(1), 237-240. doi:10.2307/3801877

Bork, E. W., West, N. E., & Walker, J. W. (1998). Cover components on long-term seasonal sheep grazing treatments in three-tip sagebrush steppe. *Journal of Range Management*, *51*(3), 293-300. doi:10.2307/4003414

Boyd, C. S., & Davies, K. W. (2012a). Differential seedling performance and environmental correlates in shrub canopy vs. interspace microsites. *Journal of Arid Environments*, *87*, 50-57. doi:10.1016/j.jaridenv.2012.06.010

Boyd, C. S., & Davies, K. W. (2012b). Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. *Environmental Management*, *50*(3), 441-450. doi:10.1007/s00267-012-9894-6

Boyd, C., Petersen, S., Gilgert, W., Rodgers, R., Fuhlendorf, S., Larsen, R., Wolfe, D., Jensen, K. C., Gonzales, P., Nenneman, M., Danvir, R., Dahlgren, D., & Messmer, T. (2011). Looking toward a brighter future for lekking grouse. *Rangelands*, *33*(6), 2-11. doi:10.2111/1551-501X-33.6.2

Cagney, J., Bainter, E., Budd, B., Christiansen, T., Herren, V., Holloran, M., Rashford, B., Smith, M., & Williams, J. (2010). *Grazing influence, objective development, and management in Wyoming's greater sage-grouse habitat with emphasis on nesting and early brood rearing*. Laramie, WY: University of Wyoming, Cooperative Extension Service.

Caldwell, M. M. (1984). Plant requirements for prudent grazing. In Natural Resource Council/National Academy of Science, *Developing Strategies for Rangeland Management* (pp. 117-152). Boulder, CO, USA: Westview Press.

Carpenter, J., Aldridge, C., & Boyce, M. S. (2010). Sage-grouse habitat selection during winter in Alberta. *The Journal of Wildlife Management*, *74*(8), 1806-1814. doi:10.2193/2009-368

Chambers, J. C., Roundy, B. A., Blank, R. R., Meyer, S. E., & Whittaker, A. (2007). What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, *77*(1), 117-145. doi:10.1890/05-1991

Chambers, J. C., Bradley, B. A., Brown, C. S., D'Antonio, C., Germino, M. J., Grace, J. B., Hardegree, S. P., Miller, R. F. & Pyke, D. A. (2013). Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, 1-16. doi:10.1007/s10021-013-9725-5

Clark, L., Hall, J., McLean, R., Dunbar, M., Klenk, K., Bowen, R., & Smeraski, C. A. (2006). Susceptibility of greater sage-grouse to experimental infection with West Nile virus. *Journal of Wildlife Diseases*, *42*(1), 14-22. doi:10.7589/0090-3558-42.1.14

Connelly, J. W., Schroeder, M. A., Sands, A. R., & Braun, C. E. (2000). Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin*, *28*(4), 967-985.

Connelly, J. W., Knick, S. T., Schroeder, M. A., & Stiver, S. J. (2004). *Conservation assessment of greater sage-grouse and sagebrush habitats*. Cheyenne, WY: Western Association of Fish and Wildlife Agencies. Retrieved from http://sagemap.wr.usgs.gov/docs/Greater_Sage-grouse_Conservation_Assessment_060404.pdf

Crawford, J. A., Olson, R. A., West, N. E., Mosley, J. C., Schroeder, M. A., Whitson, T. D., Miller, R. F., Gregg, M.A., & Boyd, C. S. (2004). Ecology and management of sage-grouse and sage-grouse habitat. *Rangeland Ecology & Management*, *57*(1), 2-19. doi:10.2111/1551-5028(2004)057[0002:EAMOSA]2.0.CO;2

Dahlgren, D. K., Chi, R., & Messmer, T. A. (2006). Greater sage-grouse response to sagebrush management in Utah. *Wildlife Society Bulletin*, *34*(4), 975-985. doi:10.2193/0091-7648(2006)34[975:GSRTSM]2.0.CO;2

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*, 63-87. doi:10.1146/annurev.es.23.110192.000431

Dalke, P. D., Pyrah, D. B., Stanton, D. C., Crawford, J. E., & Schlatterer, E. F. (1963). Ecology, productivity, and

management of sage grouse in Idaho. *Journal of Wildlife Management,* 27(4), 810-841. doi:10.2307/3798496

Davies, K. W. (2011). Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia*, *167*(2), 481-491. doi:10.1007/s00442-011-1992-2

Davies, K. W., & Sheley, R. L. (2011). Promoting native vegetation and diversity in exotic annual grass infestations. *Restoration Ecology*, *19*(2), 159-165. doi:10.1111/j.1526-100X.2009.00548.x

Davies, K. W., Bates, J. D., Johnson, D. D., & Nafus, A. M. (2009a). Influence of mowing *Artemisia tridentata* ssp. *wyomingensis* on winter habitat for wildlife. *Environmental Management*, *44*(1), 84-92. doi:10.1007/s00267-008-9258-4

Davies, K. W., Svejcar, T. J., & Bates, J. D. (2009b). Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications*, *19*(6), 1536-1545. doi:10.1890/09-0111.1

Davies, K. W., Bates, J. D., Svejcar, T. J., & Boyd, C. S. (2010). Effects of long-term livestock grazing on fuel characteristics in rangelands: An example from the sagebrush steppe. *Rangeland Ecology & Management*, *63*(6), 662-669. doi:10.2111/REM-D-10-00006.1

Davies, K. W., Bates, J. D., & Nafus, A. M. (2011a). Are there benefits to mowing Wyoming big sagebrush plant communities? An evaluation in southeastern Oregon. *Environmental Management*, *48*(3), 539-546. doi:10.1007/s00267-011-9715-3

Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., Svejcar, T. J., & Gregg, M. A. (2011b). Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation*, *144*(11), 2573-2584. doi:10.1016/j.biocon.2011.07.016

Davis, S. K., & Duncan, D. C. (1999). Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. *Studies in Avian Biology*, *19*, 211-218.

Diamond, J. M., Call, C. A., & Devoe, N. (2009). Effects of targeted cattle grazing on fire behavior of cheatgrass-dominated rangeland in the northern Great Basin, USA. *International Journal of Wildland Fire*, *18*(8), 944-950. doi:10.1071/WF08075

Diamond, J. M., Call, C. A., & Devoe, N. (2012). Effects of targeted grazing and prescribed burning on community and seed dynamics of a downy brome (*Bromus tectorum*)-dominated landscape. *Invasive Plant Science and Management*, *5*(2), 259-269. doi:10.1614/IPSM-D-10-00065.1

Doherty, K. E., Naugle, D. E., Walker, B. L., & Graham, J. M. (2008). Greater sage-grouse winter habitat selection and energy development. *The Journal of Wildlife Management*, *72*(1), 187-195. doi:10.2193/2006-454

Eng, R. L., & Schladweiler, P. (1972). Sage grouse winter movements and habitat use in central Montana. *The Journal of Wildlife Management*, *36*(1), 141-146. doi:10.2307/3799198

Evans, C. C. (1986). *The relationship of cattle grazing to sage grouse use of meadow habitat on the Sheldon National Wildlife Refuge* (Master's Thesis). University of Nevada. Reno, NV, USA.

Fischer, R. A., Reese, K. P., & Connelly, J. W. (1996a). An investigation on fire effects within xeric sage grouse brood habitat. *Journal of Range Management*, *49*(3), 194-198. doi:10.2307/4002877

Fischer, R. A., Reese, K. P., & Connelly, J. W. (1996b). Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. *The Condor*, *98*(4), 868-872. doi:10.2307/1369875

France, K. A., Ganskopp, D. C., & Boyd, C. S. (2008). Interspace/undercanopy foraging patterns of beef cattle in sagebrush habitats. *Rangeland Ecology & Management, 61*(4), 389-393. doi:10.2111/06-072.1

Frye, G. G., Connelly, J. W., Musil, D. D., & Forbey, J. S. (2013). Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. *Ecology*, *94*(2), 308-314. doi:10.1890/12-1313.1

Ganskopp, D. (2001). Manipulating cattle distribution with salt and water in large arid-land pastures: A GPS/GIS assessment. *Applied Animal Behaviour Science*, *73*(4), 251-262. doi:10.1016/S0168-1591(01)00148-4

Ganskopp, D., Svejcar, T., Taylor, F., Farstvedt, J., & Paintner, K. (1999). Seasonal cattle management in 3 to 5 year old bitterbrush stands. *Journal of Range Management*, *52*(2), 166-173. doi:10.2307/4003512

Ganskopp, D., Svejcar, T., Taylor, F., & Farstvedt, J. (2004). Can spring cattle grazing among young bitterbrush stimulate shrub growth? *Rangeland Ecology & Management*, *57*(2), 161-168. doi:10.2111/1551-5028(2004)057[0161:CSCGAY]2.0.CO;2

Gosnell, H., & Travis, W. R. (2005). Ranchland ownership dynamics in the Rocky Mountain west. *Rangeland Ecology and Management, 58*(2), 191-198. doi:10.2111/1551-5028(2005)58%3C191:RODITR%3E2.0.CO;2

Gregg, M. A., & Crawford, J. A. (2009). Survival of greater sage-grouse chicks and broods in the northern Great Basin. *The Journal of Wildlife Management*, *73*(6), 904-913. doi:10.2193/2007-410

Gregg, M. A., Crawford, J. A., Drut, M. S., & DeLong, A. K. (1994). Vegetational cover and predation of sage grouse nests in Oregon. *The Journal of Wildlife Management*, *58*(1), 162-166. doi:10.2307/3809563

Gregg, M. A., Barnett, J. K., & Crawford, J. A. (2008). Temporal variation in diet and nutrition of preincubating greater sage-grouse. *Rangeland Ecology & Management*, *61*(5), 535-542. doi:10.2111/08-037.1

Hagen, C. A. (2011). Predation on greater sage-grouse: Facts, process, and effects. *Studies in Avian Biology*, *38*, 95-100.

Hagen, C. A., Connelly, J. W., & Schroeder, M. A. (2007). A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology*, *13*(sp1), 42-50. doi:10.2981/0909-6396(2007)13[42:AMOGSC]2.0.CO;2

Hess, J. E., & Beck, J. L. (2012). Burning and mowing Wyoming big sagebrush: Do treated sites meet minimum guidelines for greater sage-grouse breeding habitats? *Wildlife Society Bulletin*, *36*(1), 85-93. doi:10.1002/wsb.92

Hockett, G. A. (2002). Livestock impacts on the herbaceous components of sage grouse habitat: A review. *Intermountain Journal of Sciences*, *8*(2), 105-114.

Holloran, M. J., & Anderson, S. H. (2005). Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *The Condor*, *107*(4), 742-752. doi:10.1650/7749.1

Holloran, M. J., Heath, B. J., Lyon, A. G., Slater, S. J., Kuipers, J. L., & Anderson, S. H. (2005). Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management*, *69*(2), 638-649. doi:10.2193/0022-541X(2005)069[0638:GSNHSA]2.0.CO;2

Johnson, G. D., & Boyce, M. S. (1990). Feeding trials with insects in the diet of sage grouse chicks. *The Journal of Wildlife Management*, *54*(1), 89-91. doi:10.2307/3808906

Kennedy, P. L., DeBano, S. J., Bartuszevige, A. M., & Lueders, A. S. (2009). Effects of native and non-native grassland plant communities on breeding passerine birds: Implications for restoration of northwest bunchgrass prairie. *Restoration Ecology*, *17*(4), 515-525. doi:10.1111/j.1526-100X.2008.00402.x

Kirol, C. P., Beck, J. L., Dinkins, J. B., & Conover, M. R. (2012). Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. *The Condor*, *114*(1), 75-89. doi:10.1525/cond.2012.110024

Klebenow, D. A. (1982). Livestock grazing interactions with sage grouse. In J. M. Peek & P. D. Dalke (Eds.), *Wildlife-livestock relationships symposium: Proceedings* (Vol. 10, pp. 113-123). Moscow, ID, USA: Forest, Wildland, and Range Experimental Station, University of Idaho. Retrieved from http://grazingforgrouse.com/sites/default/files/Klebenow%201982.pdf

Klebenow, D. A., & Gray, G. M. (1968). Food habits of juvenile sage grouse. *Journal of Range Management*, *21*(2), 80-83. doi:10.2307/3896359

Laycock, W. A. (1967). How heavy grazing and protection affect sagebrush-grass ranges. *Journal of Range Management*, *20*(4), 206-213. doi:10.2307/3896253

Mack, R. N. (1981). Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. *Agro-Ecosystems*, *7*(2), 145-165. doi:10.1016/0304-3746(81)90027-5

McAdoo, J. K., Longland, W. S., & Evans, R. A. (1989). Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. *The Journal of Wildlife Management*, *53*(2), 494-502. doi:10.2307/3801155

McAdoo, J. K., Boyd, C. S., & Sheley, R. L. (2013). Site, competition, and plant stock influence transplant success of Wyoming big sagebrush. *Rangeland Ecology & Management, 66*(3), 305-312. doi:10.2111/REM-D-12-00136.1

McArthur, E. D., & Plummer, A. P. (1978). Biogeography and management of native western shrubs: A case study, section *Tridentatae* of *Artemisia*. *Great Basin Naturalist Memoirs*, *2*, 229-243.

Meinke, C. W., Knick, S. T., & Pyke, D. A. (2009). A spatial model to prioritize sagebrush landscapes in the Intermountain West (USA) for restoration. *Restoration Ecology*, *17*(5), 652-659. doi:10.1111/j.1526-100X.2008.00400.x

Miller, R. F., & Tausch, R. J. (2001). The role of fire in pinyon and juniper woodlands: A descriptive analysis. In K.E.M. Galley and S. G. Coloff (Eds.), *Proceedings of the invasive species workshop: The role of fire in the control and spread of invasive species* (Miscellaneous Publication No. 11, pp. 15-30). Tallahassee, FL, USA: Tall Timbers Research Station. *Available at: http://oregonstate.edu/dept/EOARC/sites/default/files/researchhome/documents/461.pdf*

Miller, R. F., & Eddleman, L. L. (2001). *Spatial and temporal changes of sage grouse habitat in the sagebrush biome* (Bulletin No. 151). Corvallis, OR, USA: Oregon State University Agricultural Experiment Station. Retrieved from http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/20881/tb151.pdf

Miller, R. F., Svejcar, T. J., West, N. E. (1994). Implications of livestock grazing in the Intermountain sagebrush region: Plant composition. In M. Vavra, W. A. Laycock & R. D Pieper, (Eds.), *Ecological implications of herbivory in the west* (pp. 101-146). Denver, CO: Society for Range Management.

Miller, R. F., Bates, J. D., Svejcar, A. J., Pierson Jr, F. B., & Eddleman, L. E. (2005). *Biology, ecology, and management of western juniper (Juniperus Occidentalis)* (Bulletin No. 152). Corvallis, OR, USA: Oregon State University Agricultural Experiment Station. Retrieved from http://juniper.oregonstate.edu/bibliography/documents/phpQ65pOk_tb152.pdf

Monaco, T. A., Osmond, T. M., & Dewey, S. A. (2005). Medusahead control with fall-and spring-applied herbicides on northern Utah foothills. *Weed Technology*, *19*(3), 653-658. doi:10.1614/WT-04-202R2.1

Mueggler, W. F. (1950). Effects of spring and fall grazing by sheep on vegetation of the Upper Snake River Plains. *Journal of Range Management*, *3*(4), 308-315. doi:10.2307/3894355

NIFC (National Interagency Fire Center). (2012). *National Interagency Fire Center*. Retrieved from http://www.nifc.gov/fireInfo/fireInfo_statistics.html.

Naugle, D. E., Aldridge, C. L., Walker, B. L., Cornish, T. E., Moynahan, B. J., Holloran, M. J., Brown, K., Johnson, G. D., Schmidtman, E. T., Mayer, R. T., Kato, C. Y., Matchett, M. R., Christiansen, T. J., Cook, W. E., Creekmore, T., Falise, R. D., Rinkes, E. T., & Boyce, M. S. (2004). West Nile virus: Pending crisis for greater sage-grouse. *Ecology Letters*, *7*(8), 704-713. doi:10.1111/j.1461-0248.2004.00631.x

Naugle, D. E., Aldridge, C. L., Walker, B. L., Doherty, K. E., Matchett, M. R., McIntosh, J., Cornish, T. E., & Boyce, M. S. (2005). West Nile virus and sage-grouse: What more have we learned? *Wildlife Society Bulletin*, *33*(2), 616-623. doi:10.2193/0091-7648(2005)33[616:WNVASW]2.0.CO;2

Naugle, D. E., Doherty, K. E., Walker, B. L., Holloran, M. J., & Copeland, H. E. (2011). Energy development and greater sage-grouse. In S.T. Knick and J.W. Connelly (Eds.), *Studies in Avian Biology* (*Vol 38*, pp. 489-503). Berkeley CA, USA: University of California Press.

Neel, L.A. (1980). *Sage grouse response to grazing management in Nevada* (Master's thesis). University of Nevada, Reno, NV, USA.

Olson, R. A., & Whitson, T. D. (2002). Restoring structure in late-successional sagebrush communities by thinning with tebuthiuron. *Restoration Ecology*, *10*(1), 146-155. doi:10.1046/j.1526-100X.2002.10116.x

Olson, R., Hansen, J., Whitson, T., & Johnson, K. (1994). Tebuthiuron to enhance rangeland diversity. *Rangelands*, *16*(5), 197-201.

Peterson, J. G. (1970). The food habits and summer distribution of juvenile sage grouse in central Montana. *The Journal of Wildlife Management*, *34*(1), 147-155. doi:10.2307/3799502

Pierson, F. B., Bates, J. D., Svejcar, T. J., & Hardegree, S. P. (2007). Runoff and erosion after cutting western juniper. *Rangeland Ecology & Management*, *60*(3), 285-292. doi:10.2111/1551-5028(2007)60[285:RAEACW]2.0.CO;2

Pyne, S. J., Andrews, P. L., & Laven, R. D. (1996). *Introduction to wildland fire* (2nd ed.). New York City, NY, USA: John Wiley and Sons.

Rafferty, D. L., & Young, J. A. (2002). Cheatgrass competition and establishment of desert needlegrass seedlings. *Journal of Range Management*, *55*(1), 70-72. doi:10.2307/4003265

Rasmussen, D. I., & Griner, L. A. (1938). Life history and management studies of the sage grouse in Utah, with special reference to nesting and feeding habits. In *Transactions of the North American Wildlife Conference* (Vol. 3, pp. 852-864). Washington, DC, USA: American Wildlife Institue.

Remington, T. E., & Braun, C. E. (1985). Sage grouse food selection in winter, North Park, Colorado. *The Journal of Wildlife Management*, *49*(4), 1055-1061. doi:10.2307/3801395

Remington, T. E., & Braun, C. E. (1988). Carcass composition and energy reserves of sage grouse during winter. *Condor*, *90*(1), 15-19. doi:10.2307/1368427

Reynolds, T. D., & Trost, C. H. (1980). The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. *Journal of Range Management,* 33(2), 122-125. doi:10.2307/3898425

Reynolds, T., & Trost, C. (1981). Grazing, crested wheatgrass, and bird populations in southeastern Idaho. *Northwest Science*, *55*(3), 225-234.

Rhodes, E. C., Bates, J. D., Sharp, R. N., & Davies, K. W. (2010). Fire effects on cover and dietary resources of sage-

grouse habitat. *The Journal of Wildlife Management*, *74*(4), 755-764. doi:10.2193/2009-143

Riegel, G. M., Miller, R. F., Skinner, C. N., & Smith, S. E. (2006). Northeastern plateaus bioregion. In N. G. Sugihara, J. W. van Wagtendonk, J. Fites-Kaufmann, K. E. Shaffer & A. E. Thode (Eds.), *Fire in California's ecosystems* (pp. 225-263). Berkeley, CA, USA: University of California Press.

Rimbey, N. R., Torell, L. A., & Tanaka, J. A. (2007). Why grazing permits have economic value. *Journal of Agricultural and Resource Economics, 32*(1), 20-40.

Schroeder, M. A., J. R. Young, & C. E. Braun. (1999). Sage grouse *(Centrocercus urophasianus).* In A. Poole & F. Gill (Eds.), *The birds of North America* No. 425. Philadelphia, PA, USA: The Birds of North America.

Schmelzer, L., Perryman, B., Bruce, B., Schultz, B., McAdoo, K., McCuin, G., Swanson, S., Wilder, J., & Conley, K. (In Press). Reducing cheatgrass (*Bromus tectorum* L.) fuel loads using fall cattle grazing: A case study. *Professional Animal Scientist*.

Schuman, G. E., Reeder, J. D., Manley, J. T., Hart, R. H., & Manley, W. A. (1999). Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. *Ecological Applications*, *9*(1), 65-71. doi:10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2

Sika, J.L. (2006). *Breeding ecology, survival rates, and causes of mortality of hunted and nonhunted greater sage-grouse in central Montana* (Master's thesis). Montana State University, Bozeman, MT, USA. Retrieved from http://scholarworks.montana.edu/xmlui/bitstream/handle/1/2279/SikaJ1206.pdf?sequence=1

Smith, B., Sheley, R. L., & Svejcar, T. J. (2012). *Grazing invasive annual grasses: The green and brown guide*. Burns, OR, USA: Eastern Oregon Agricultural Research Center. Retrieved from http://www.weedcenter.org/technicalwebinars/documents/SheleyPubs/GrazingAnnualGrasses.pdf

Sneva, F. A., Rittenhouse, L. R., Tueller, P. T., & Reece, P. (1984). *Changes in protected and grazed sagebrush-grass in eastern Oregon, 1937 to 1974* (Bulletin No. 663). Corvallis, OR: Oregon State University, Agricultural Experiment Station. Retrieved from http://extension.oregonstate.edu/catalog/html/sb/sb663-e/

Stevens, B. S., Connelly, J. W., & Reese, K. P. (2012a). Multi-scale assessment of greater sage-grouse fence collision as a function of site and broad scale factors. *The Journal of Wildlife Management*, *76*(7), 1370-1380. doi:10.1002/jwmg.397

Stevens, B. S., Reese, K. P., Connelly, J. W., & Musil, D. D. (2012b). Greater sage-grouse and fences: Does marking reduce collisions? *Wildlife Society Bulletin, 36*(2), 297-303. doi:10.1002/wsb.142

Strand, E., Launchbaugh, K., Limb, R., & Torell, A. (2014). Livestock grazing effects on fuel loads for wildland fire in sagebrush dominated ecosystems. *Journal of Rangeland Applications, 1*.

Sveum, C. M., Edge, W. D., & Crawford, J. A. (1998). Nesting habitat selection by sage grouse in south-central Washington. *Journal of Range Management*, *51*(3), 265-269. doi:10.2307/4003409

Tanaka, J. A., & Workman, J. P. (1990). Optimal vegetation conversion - how much, how often? Rangelands 12(1), 33-36.

Tanaka, J. A., Torell, L. A., & Brunson, M. W. (2011). Chapter 9: A social and economic assessment of rangeland conservation practices. In D. E. Briske, (ed.). *Conservation benefits of rangeland practices: Assessment, recommendations, and knowledge gaps* (pp. 371-422). Washington, DC, USA: US Department of Agriculture, Natural Resources Conservation Service. Retrieved from http://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/technical/?cid=stelprdb1045811

Taylor, R. L., Tack, J. D., Naugle, D. E., & Mills, L. S. (2013). Combined effects of energy development and disease on greater sage-grouse. *PLoS ONE*, 8(8): e71256. DOI: 10.1371/journal.pone.0071256

Thacker, E. T. (2010). *Greater sage-grouse seasonal ecology and responses to habitat manipulations in northern Utah* (Doctoral dissertation). Utah State University, Logan, UT, USA. Retrieved from http://digitalcommons.usu.edu/cgi/viewcontent.cgi?article=1703&context=etd

Torell, L. A. (2002). *Ranch-level impacts of changing grazing policies on BLM land to protect the Greater Sage-Grouse: Evidence from Idaho, Nevada and Oregon*. Caldwell, ID: Policy Analysis Center for Western Public Lands. Retrieved from http://sagemap.wr.usgs.gov/Docs/sage-grouse_econ.pdf

Torell, L. A., Rimbey, N. R., Ramirez, O. A., & McCollum, D. W. (2005). Income earning potential versus consumptive amenities in determining ranchland values. *Journal of Agricultural and Resource Economics, 30*(3), 537-560.

Torell, L. A., Rimbey, N. R., Tanaka, J. A., Taylor, D. T., & Wulfhorst, J. D. (2014). Ranch level economic impact analysis for public lands: a guide to methods, issues, and applications. *Journal of Rangeland Applications, 1*.

USFWS (United States Fish and Wildlife Service). (2010). Twelve-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. *Federal Register, 75*, 13910-14014. Mar. 4, 2010. Available online at: https://www.fws.gov/wyominges/PDFs/Findings/SageGrouse/FR03052010.pdf

Wallestad, R. O. (1971). Summer movements and habitat use by sage grouse broods in central Montana. *The Journal of Wildlife Management*, *35*(1), 129-136. doi:10.2307/3799881

Wallestad, R., & Eng, R. L. (1975). Foods of adult sage grouse in central Montana. *The Journal of Wildlife Management*, *39*(3), 628-630. doi:10.2307/3800409

Walker, B. L., & Naugle, D. E. (2011). West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. *Studies in Avian Biology,* 38, 127-142.

Welch, B. L., Wagstaff, F. J., & Roberson, J. A. (1991). Preference of wintering sage grouse for big sagebrush. *Journal of Range Management*, *44*(5), 462-465. doi:10.2307/4002745

West, N. E. (1989). *Vegetation types of Utah*. In K.L. John (ed.), *Rangeland Resources of Utah* (pp. 18-56). Logan, UT, USA: Utah State University, Cooperative Extension Service.

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, *42*(4), 266-274. doi:10.2307/3899492

Whisenant, S. G. (1990). Changing fire frequencies on Idaho's Snake River Plains: Ecological and management implications. In E. D. McArthur, E. M. Romney, S. D. Smith, & P. T. Tueller (Eds.), *Proceedings from the symposium on cheatgrass invasion, shrub dieoff and other aspects of shrub biology and management* (General Technical Report No. 276; pp. 4-10). Ogden, UT, USA: US Department of Agriculture, Forest Service, Intermountain Research Station. Retrieved from http://www.treesearch.fs.fed.us/pubs/40669

Workman, J. P. (1986). Range economics. New York City, NY, USA: Macmillan Publishing Company.

Wright, H. A. (1970). A method to determine heat-caused mortality in bunchgrasses. *Ecology*, *51*(4), 582-587. doi:10.2307/1934038

Wright, H. A., & Bailey, A. W. (1982). *Fire ecology: United States and southern Canada*. New York City, NY, USA: Wiley.

Young, K. R., & Mangold, J. M. (2008). Medusahead outperforms squirreltail through interference and growth rate. *Journal of Invasive Plant Science and Management*, *1*(1), 73-81. doi:10.1614/IPSM-07-021.1

Young, J. A., & Sparks, B. A. (1985). *Cattle in the cold desert*. Reno, NV, USA: University of Nevada Press.

Ziegenhagen, L. L., & Miller, R. F. (2009). Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. *Western North American Naturalist*, *69*(2), 195-205. doi:10.3398/064.069.0208

Cattle Distribution Under Intensive Herded Management

PAUL J. BUTLER

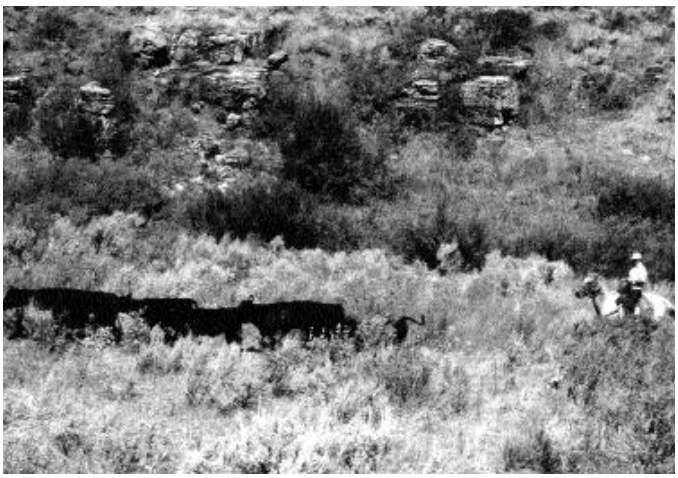
The trial using a Peruvian herder to control cattle on the Caribou National Forest is one of the first attempts in recent years to introduce a variation of intensive cattle herding onto native rangelands in the Western United States. By sheperding cattle seven days a week, riparian areas can be protected from long-term streambank degradation.

A clear distinction needs to be made between a rider and a herder for those who might think they are one and the same. Nearly all large cattle allotments throughout the West have a rider, generally a cowboy hired to fix fence, place salt, move cows from unit to unit, and police herd health. A herder's primary job is to herd livestock, whether it be sheep or in this case cattle. Generally, there is too much work to be done on a cattle allotment for one individual to do both jobs.

The herder trial on the Caribou National Forest was implemented in southeast Idaho on the Portneuf Cattle Allotment which lies 20 miles east of Pocatello. Past conditions on the allotment that prompted us to look towards more intensive management included overuse of riparian vegetation, streambank trampling, streambank shearing, lack of effective fence controls, unacceptable cattle drift into unauthorized units, and low levels of residual vegetation for bank protection during spring runoff. Drift outside of authorized units impacted ungrazed units, previously grazed units, and neighboring allotments.

The Portneuf Cattle Association and Forest Service recognized the need to intensify the grazing management on the allotment. The association was building an average of 1 1/2 miles of fence and 3 water developments per year. Problems still existed in properly using many of the riparian areas on the allotment in spite of the fact that a full-time cowboy was hired to ride the allotment. Cattle were hanging in riparian zones until forage was utilized, then they would move out to the uplands, which is a common characteristic of cattle. Even when units were 100% cleaned once they had been grazed, unauthorized drift-back often meant that the unit received little to no rest.

Very little documentation exists on the effects of herding cattle. It was decided that a trial would be implemented to ascertain the effectiveness of using a herder in concert with existing structural range improvements in order to protect sensitive riparian zones. The overall goal was to reduce the amount of time cattle spent in riparian areas by herding them into the uplands on a daily basis.



Peruvian herder Maurico Aquino moving cattle off stream after they have watered.

History of the Initiative

I like to think that one of our primary jobs as public land managers is in education. The ranching community has come a long way in the last 20 years, but they often need convincing when we propose management changes that are out-of-the-ordinary. How do you convince a grazing association to spend more money on the management of their public land grazing allotment? You lead by example. In spite of heavy criticism and opposition by the Forest Service, the Westside District forged ahead with a cost-share proposal to get the program moving.

Perhaps we should get this argument out of the way right now. The proposal was not popular in Forest Service circles because it was perceived that we were paying the ranchers to herd their cows. The fact is that the investment, under a cost-share program, showed the grazing association that the Forest Service was indeed serious about a cooperative relationship. In other words, we are not here to force you to our will, we are here to lead you in progressive, up-to-date range management. The Portneuf Grazing Association voted to continue the herder program on their own after two years. Now, four seasons later, it has become a show-case for intensive grazing management.

Contributions for the trial amounted to $2900.00 from the Portneuf Grazing Association, $1430.00 from the Forest Service, and $500.00 from the Idaho Department of Fish and Game. In the end, the Forest Service was not allowed to contribute directly to the grazing association, so Utah State University (USU) agreed to broker the dollars and also participate in the program. USU helped identify areas of monitoring needs and provided expertise in translating herder instructions to Spanish.

The Portneuf Cattle Allotment covers 26,000 acres of predominantly rolling topography. Elevation varies from 5,600 to 7,000 feet. The allotment is grazed by two separate herds of cattle each having five grazing units. The herder trial was implemented using the northern herd on the Toponce Division.

Four hundred and fifty cow-calf pairs graze this division from June 1 to October 10. Each unit has sensitive riparian areas within its boundaries.

In early 1996, a Peruvian cowboy was hired by the Portneuf Cattle Association through an agricultural service. The trial began with four main objectives:

1. Determine if herding is more effective than additional fencing.
2. Compare economics of herding vs additional fencing.
3. Determine benefits to riparian zones.
4. Monitor and document results.

Cattle normally come to water by mid-morning, shade-up, then move off to feed in the afternoon.

Effectiveness

At the beginning of each season, the herder was given a list of instructions in both Spanish and English, an accurate and easy-to-read map with all structural range improvements and delineated units, and a calendar or *diario registro* with which to record his daily monitoring observations. Questions were answered on the *registro* such as "How many cows did you herd away from the streams today?, or How many cows did you find outside the unit today?" Weekly visits were made to the site either by forest officers or association members to ensure that the results of the trial would be valid.

Cattle normally come to water by mid-morning, shade-up, then move off to feed in the afternoon. Often they will get a drink of water before beginning the afternoon feeding. This aspect of their behavior makes it necessary for the cows to have alternative water sources available for their use once they are herded away from riparian zones. Much of the original thought process in developing this program came from managing sheep. On the Westside Ranger District, sheep are allowed to water for one hour per day on live streams. The sheepherder is required to immediately move the sheep off water before they can shade-up. This process can work just as well with cattle, provided that they can be moved to a location where they have forage, alternative water, and security.

The herder was instructed to allow the cows to come to water, but beginning about 10 a.m., or when the balance of the herd had watered, to gather the herd off the stream and gently ease them back to the uplands away from the riparian area. When an area of good forage was found, settle the herd and ensure that they are either shading up or feeding before leaving. This will generally prevent the herd from immediately returning to the stream. During the cooler hours of the day when cattle are feeding, the herder was instructed to patrol areas of drift where cows normally escaped from the designated unit.

Early on it was discovered that too much reliance on uplands could lead to watershed degradation. Riparian zones often comprise only one to three percent of the community types on western rangelands. However, they contribute, or have the ability to contribute, a large share of the available forage. This makes them key in the management of any grazing allotment. It is important to remember that the carrying capacity for a grazing allotment is generated using the forage available within the riparian zone. The herder program worked so well during the first year that very little use was being made in the riparian zones and higher levels of use were being made in the uplands. It was found that excellent results could be realized by herding the cattle off the streams for the first 75% of the unit use and allowing them to graze the riparian bottoms for the remaining 25% of the time allowed in that unit. This amounted to a high intensity, low duration system on the riparian zones.

Monitoring results showed that the program was successful only if the herder showed a consistent DAILY presence on the allotment. When the herder moved cattle off the streams on a daily basis, less than four percent of the herd returned the following day. When the herder missed a day of riding, 16% to 24% of the herd returned to the stream.

Cattle quickly acclimate themselves to the presence of a herder. Once the herder misses even as much as one day, the cows quickly become unsettled and often refuse to be herded.

When herd death losses were tallied after the first year, the herder program had actually paid for itself in reduced losses. This was attributed to the increased presence on the allotment. Losses in 1996 were less than a third of the 10-year average.

Beneficial Results to Riparian Zones

While it is still too early to confirm through permanent trend studies that species composition is in an upward trend, photographs point out that the program is successful in reducing vegetation use along riparian corridors, reducing streambank trampling and shearing, and providing residual streambank protection after grazing for periods of spring runoff.

Not only does this method reduce the amount of time spent in riparian zones by cattle, it helps to ensure grazing units receive the appropriate amount of time necessary for them to regrow and maintain high levels of health and vigor when drift into unauthorized units or back into units already grazed is controlled. The amount and kind of forage will normally be improved when intensive management is applied to native rangelands. Monitoring shows us quickly moving in the right direction.

FOUR FACTORS NEEDED FOR SUCCESS

Topography

Steep slopes make moving cattle away from riparian zones difficult. Many current cattle allotments were once sheep allotments where suitable sheep range over 25% slope could once be expected to be grazed. Cattle will not utilize steep slopes on a regular basis until forage in riparian bottoms that



Photo of stream prior to herder program showing degraded stream banks with no residual bank protection.

is easily available and more palatable is fully utilized. It is very difficult to move cattle out of steep valleys on a daily basis not to mention that damage to watersheds by repeated trailing of herds may be more detrimental to the resource than if they were left alone. Allotments where topography is gentle are good candidates for an intensive herder program.

Fences

Some fence controls must be in place. The herder cannot be everywhere all the time. This program is not dependent on fences, rather it complements existing structural range improvements.

Alternative Water

If alternative water sources are not developed, the cows will not stay away from the riparian zones and may, in fact, beat the herder back to the stream.

Consistent Presence

Results prove that a consistent daily presence on the cattle allotment alleviated riparian zone pressure and quickly reversed livestock use that was not consistent with progressive and intensive rangeland management. Daily management of the herd was necessary to keep them from taking advantage of the absence of the herder. Once the herder missed a day of moving cattle, they quickly reverted back to their old ways of hanging on the creeks. This program did not employ a rider. It employed a full-time herder.

SUMMARY

Intensive cattle herding is an important tool that can be employed in the proper management of riparian zones which are a highly sensitive and vulnerable rangeland community. It is not the cure-all for poor management and it does not absolve us when we ignore the need to develop structural rangeland improvements such as fences and water developments. However, it may be one of the most effective complementary tools available to us in managing the rangelands of North America.

Author is Supervisory Range Conservationist with the Caribou National Forest, Westside Ranger District, Pocatello, Idaho.

This paper was presented at the 1998 SRM Annual Meeting in Guadalajara, Mexico.

USDA United States Department of Agriculture

Using Resilience and Resistance Concepts to Manage Threats to Sagebrush Ecosystems, Gunnison Sage-Grouse, and Greater Sage-Grouse in Their Eastern Range: A Strategic Multi-Scale Approach

Jeanne C. Chambers, Jeffrey L. Beck, Steve Campbell, John Carlson, Thomas J. Christiansen, Karen J. Clause, Jonathan B. Dinkins, Kevin E. Doherty, sLIVDDNktQ1PNM/wVLEaLV1NLsDNNDmaDN3DeLv/BMaDNN1w□ Laurie L. Kurth, Jeremy D. Maestas, Mary Manning, Kenneth E. Mayer, Brian A. Mealor, Clinton McCarthy, Marco A. Perea, and David A. Pyke



Forest Service

Rocky Mountain Research Station

General Technical Report RMRS-GTR-356

December 2016

Chambers, J.C.; Beck, J.L.; Campbell, S.; Carlson, J.; Christiansen, T.J.; Clause, K.J.; Dinkins, J.B.; Doherty, K.E.; Griffin, K.A.; Havlina, D.W.; Henke, K.F.; Hennig, J.D.; Kurth, L.L.; Maestas, J.D.; Manning, M.; Mayer, K.E.; Mealor, B.A.; McCarthy, C.; Perea, M.A.; Pyke, D.A. 2016. **Using resilience and resistance concepts to manage threats to sagebrush ecosystems, Gunnison sage-grouse, and Greater sage-grouse in their eastern range: A strategic multi-scale approach.** Gen. Tech. Rep. RMRS-GTR-356. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 143 p.

Abstract

This report provides a strategic approach developed by a Western Association of Fish and Wildlife Agencies interagency working group for conservation of sagebrush ecosystems, Greater sage-grouse, and Gunnison sage-grouse. It uses information on (1) factors that influence sagebrush ecosystem resilience to disturbance and resistance to nonnative invasive annual grasses and (2) distribution and relative abundance of sage-grouse populations to address persistent ecosystem threats, such as invasive annual grasses and wildfire, and land use and development threats, such as oil and gas development and cropland conversion, to develop effective management strategies. A sage-grouse habitat matrix links relative resilience and resistance of sagebrush ecosystems with modeled sage-grouse breeding habitat probabilities to help decisionmakers assess risks and determine appropriate management strategies at both landscape and site scales. Areas for targeted management are assessed by overlaying matrix components with Greater sage-grouse Priority Areas for Conservation and Gunnison sage-grouse critical habitat and linkages, breeding bird concentration areas, and specific habitat threats. Decision tools are discussed for determining the suitability of target areas for management and the most appropriate management actions. A similar approach was developed for the Great Basin that was incorporated into the Federal land use plan amendments and served as the basis of a Bureau of Land Management Fire and Invasives Assessment Tool, which was used to prioritize sage-grouse habitat for targeted management activities.

Keywords: sagebrush habitat, Greater sage-grouse, Gunnison sage-grouse, persistent ecosystem threats, land use and development threats, climate change, management prioritization, conservation, restoration

a4PWIdP)4ckPIP . Expansive big sagebrush in sage-grouse Management Zone II (photo by M. Evans) with male Greater sage-grouse on road inset (photo by C.P. Kirol).
Inside Cover Photo. Sage-grouse lek in Sublette County, Wyoming (photo by T. Christiansen).
Back Cover Photo. Male Greater sage-grouse in a sagebrush ecosystem in Management Zone I (photo by C. Duchardt).

Authors

Jeanne C. Chambers, Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, Reno, Nevada.

Jeffrey L. Beck, Associate Professor, Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming.

Steve Campbell, Soil Scientist, USDA Natural Resources Conservation Service, Portland, Oregon.

John Carlson, Management Zone I Greater Sage-Grouse Lead, USDI Bureau of Land Management, Billings, Montana.

Thomas J. Christiansen, Sage-Grouse Program Coordinator, Wyoming Game & Fish Department, Green River, Wyoming.

Karen J. Clause, Rangeland Management Specialist, USDA Natural Resources Conservation Service, Pinedale, Wyoming.

Jonathan B. Dinkins, Postdoctoral Research Associate, Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming.

Kevin E. Doherty, Wildlife Biologist, U.S. Fish and Wildlife Service, Lakewood, Colorado.

Kathleen A. Griffin, Grouse Conservation Coordinator, Colorado Parks and Wildlife, Grand Junction, Colorado.

[illegible], Fire Ecologist, USDI Bureau of Land Management, National Interagency Fire Center, Boise, Idaho.

[illegible], Natural Resource Specialist, USDI Bureau of Land Management, Cheyenne, Wyoming.

[illegible], Spatial and Data Technician, Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming.

Laurie L. Kurth, Applied Fire Ecologist, USDA Forest Service, Fire and Aviation Management, Washington, DC.

Jeremy D. Maestas, Sagebrush Ecosystem Specialist, USDA Natural Resources Conservation Service, Redmond, Oregon.

Mary Manning, Regional Vegetation Ecologist, USDA Forest Service, Missoula, Montana.

Kenneth E. Mayer, Wildlife Ecologist, Western Association of Fish and Wildlife Agencies, Sparks, Nevada.

Brian A. Mealor, Associate Professor, Extension Weed Specialist, Department of Plant Sciences, University of Wyoming, Laramie, Wyoming.

[illegible], Retired Wildlife Biologist, Region 4, USDA Forest Service, Ogden, Utah.

Marco A. Perea, Fire Management Specialist, USDI Bureau of Land Management, Lakewood, Colorado.

David A. Pyke, Research Ecologist, U.S. Geological Survey, Forest & Rangeland Ecosystem Science Center, Corvallis, Oregon.

Acknowledgments

We thank the Western Association of Fish and Wildlife Agencies, Great Basin Landscape Conservation Cooperative, and Bureau of Land Management for financial support of this effort. We also thank the numerous resource specialists who provided input into the ecological type descriptions, state-and-transition models, and fire and fuels management strategies, and who reviewed a draft of this report. Cameron Aldridge, Steve Hanser, Jane Mangold, and Mary Rowland provided valuable comments on the report.



All Rocky Mountain Research Station publications are published by U.S. Forest Service employees and are in the public domain and available at no cost. Even though U.S. Forest Service publications are not copyrighted, they are formatted according to U.S. Department of Agriculture standards and research findings and formatting cannot be altered in reprints. Altering content or formatting, including the cover and title page, is strictly prohibited.

Contents

1. Purpose and Use of this Document 1

2. Introduction 2

3. Climatic Regimes and Vegetation Types 4

4. Threats to Sagebrush Ecosystems, Greater Sage-Grouse, and Gunnison Sage-Grouse 13
- 4.1 Persistent Ecosystem Threats 13
- 4.2 Climate Change 22
- 4.3 Land Use and Development Threats 25

5. Resilience to Disturbance and Resistance to Nonnative Invasive Plant Species 36

6. Integrating Resilience and Resistance Concepts with Sage-Grouse Habitat Requirements to Prioritize Areas for Management and Inform Management Strategies 39
- 6.1 Sage-grouse Breeding Habitat Probabilities and Population Indices 39
- 6.2 Soil Temperature and Moisture Regimes as Indicators of Ecosystem Resilience and Resistance 46
- 6.3 Sage-Grouse Habitat Resilience and Resistance Matrix 51

7. Delineating Habitats for Targeted Management Intervention at the Ecoregional/Management Zone Scale 59
- 7.1 Assessing Target Areas for Sage-Grouse Habitat Management – Key Data Layers 59
- 7.2 Assessing Target Areas for Sage-Grouse Habitat Management – Overlaying data layers 63

8. Determining Appropriate Management Treatments at Local Scales 72
- 8.1 Steps in the Process 72
- 8.2 Examples of How to Apply the Concepts and Tools 75
- 8.3 Monitoring and Adaptive Management 88
- 8.4 Sources of Management Information 89

9. Conclusions 90

References 91

Appendix A1. Definitions of Terms Used in This Document 110

Appendix A2. Explanation of Soil Temperature and Moisture Regime Data 112

Appendix A3. Methods for Determining the Predominant Ecological Types 115

Appendix A4. Data Sources for the Maps in This Report 123

Appendix A5. Explanation of the Use of Landscape Measures to Describe Sagebrush Habitat 126

Appendix A6. State-and-Transition Models for the Predominant Sagebrush Ecological Types in the West-Central Semiarid Prairies, Western Cordillera, and Cold Desert 127

Appendix A7. Informing Wildfire and Fuels Management Strategies to Conserve Sagebrush Ecosystems and Sage-Grouse 138

Appendix A8. Informing Management Strategies in the Face of Climate Change 142

1. Purpose and Use of this Document

The primary purpose of this report is to (1) facilitate large-scale prioritization of limited resources across administrative boundaries to address persistent ecosystem threats, (2) provide a unifying framework to communicate relative risks, and (3) assist in determining appropriate management strategies to promote both species and ecosystem persistence at multiple scales. An approach is provided that links information on ecosystem resilience to disturbance and resistance to invasive plant species with data on species habitat and population abundance. A key aspect of the process is prioritizing areas for management at the scale of ecoregions or Management Zones. Once these priority areas for management are determined, they are used to inform budget prioritization and to ensure consistent allocation of funds.

Ecoregion or Management Zone priorities are stepped down to local scales by engaging managers and stakeholders to refine priorities based on higher resolution geospatial products and more detailed species information and to identify opportunities to leverage partner resources. The ultimate goal is to ensure that enough of the right actions are implemented in the right places, consistently through time, to maintain the distribution and abundance of functioning sagebrush ecosystems and sage-grouse. This approach is consistent with prioritizations and management strategies already being applied by local land managers, but places those actions into a broader context and helps to justify the need to sustain or enhance conservation and restoration investments.

This document is divided into parts that can be used by the reader to gain an understanding of (1) the biophysical characteristics of sagebrush ecosystems and threats to sagebrush ecosystems, Greater sage-grouse (*Centrocercus urophasianus,* hereafter GRSG), and Gunnison sage-grouse (*Centrocercus minimus*, hereafter GUSG), (2) the key concepts and approach used to prioritize areas for management and develop effective management strategies, and (3) the necessary information for determining appropriate management treatments. Users of the document will find the rationale for this report in section "2. Introduction." Individuals who are unfamiliar with the biophysical characteristics of sagebrush ecosystems and threats to sagebrush ecosystems, GRSG, and GUSG can access that information in sections "3. Climatic Regimes and Vegetation Types," and "4. Threats to Sagebrush Ecosystems, Greater Sage-Grouse, and Gunnison Sage-Grouse," respectively. Those who are familiar with sagebrush ecosystems and their threats but lack an understanding of resilience to disturbance and resistance to invasive annual grasses can obtain that information in section "5. Resilience to Disturbance and Resistance to Nonnative Invasive Plant Species." The key elements of the approach are in sections "6. Integrating Resilience and Resistance Concepts with Sage-Grouse Habitat Requirements to Prioritize Areas for Management and Inform Management Strategies," and "7. Delineating Habitats for Targeted Management Intervention at the Ecoregional/Management Zone Scale," and will be of interest to all users. Section "8. Determining Appropriate Management Treatments at the Local Scales" provides information and examples and also will be of general interest.

Geospatial data, maps, and models are provided through the U.S. Geological Survey ScienceBase (https://www.sciencebase.gov/catalog/item/576bf69ce4b07657d1a26ea2) and BLM Landscape Approach Data Portal (http://www.blm.gov/wo/st/en/prog/more/Landscape_Approach/dataportal.html) to assist managers in implementing the resilience-based approach described herein. Handbooks and guides for implementing

this approach are available for the western portion of the sagebrush biome that can be adapted to the eastern portion of the sagebrush biome (Miller et al. 2014, 2015; Pyke et al. 2015a,b).

2. Introduction

Sagebrush (*Artemisia* spp.) ecosystems are among the largest and most imperiled ecosystems in North America (Noss et al. 1995). Sage-grouse and the more than 350 other species that rely on sagebrush ecosystems (Suring et al. 2005) face widespread habitat loss due to multiple, interacting threats. The GRSG has been considered for Federal regulatory protections under the Endangered Species Act eight times (USFWS 2015). The GUSG was designated as threatened (USFWS 2014a) with 1.4 million acres (566,000 ha) designated as critical habitat under the Endangered Species Act in 2014 (USFWS 2014b). Concern over GRSG and GUSG and their associated habitats has set in motion Federal and State land management policy changes and proactive conservation actions to address threats within the realm of management control (Western Governors Association 2015). However, persistent ecosystem threats, such as invasive species and altered disturbance regimes, interact with land uses and development threats, such as oil and gas development and cropland conversion, and remain widespread issues that require sustained management effort (see Goble et al. 2012; Scott et al. 2010). To address these threats, a strategic, multi-scale approach based on resilience science has been developed for the western portion of the GRSG range (Chambers et al. 2014a). This approach provides the framework for wildland fire operations, post-fire rehabilitation, fuels management, and restoration/recovery strategies, and has been used as the basis for prioritization of GRSG conservation resources at national and regional scales (USDA NRCS 2015b; USDI BLM 2014). In this report, we develop a similar approach for the GUSG range and the eastern portion of GRSG range that can be used to help prioritize areas for management and determine the most effective management strategies based on an area's resilience to disturbance and resistance to nonnative invasive plants, particularly invasive annual grasses.

Two different types of threats impact sagebrush ecosystems and sage-grouse in the eastern portion of the range. Persistent ecosystem threats—invasion of nonnative invasive plants, altered fire regimes, conifer expansion, and climate change (Miller et al. 2011)—are difficult to regulate and must be managed using ecologically based approaches (Boyd et al. 2014b; Evans et al. 2013). In contrast, threats due to land uses and development—energy development, conversion to cropland, livestock grazing, mining, and urban, suburban, and exurban development—can be regulated on public land. These two threats often interact with each other. For example, oil and gas development can increase the spread of invasive annual grasses and potential for wildfire, and invasive annual grasses can increase the difficulty of restoring sites impacted by oil and gas development (Mealor et al. 2013). Many land use and development threats have been extensively studied or reviewed in recent years (see Hanser et al. 2011; Knick and Connelly 2011; Manier et al. 2014). In this report, we focus on persistent ecosystem threats and the secondary effects of land use and development on ecosystems such as invasion of nonnative plant species. Importantly, the same types of ecologically based approaches used to manage persistent ecosystem threats can be used to minimize impacts and increase restoration effectiveness of habitats affected by land use and development.

Resilience science has been used to provide a conceptual basis for conservation planning (Curtin and Parker 2014; Fischer et al. 2009). Spatially explicit knowledge of how ecosystem resilience and resistance vary across large landscapes can provide the basis for threat management (Rowland and Wisdom 2009; Wisdom and Chambers 2009). ***Resilient*** ecosystems have the capacity to ***reorganize and regain*** their fundamental structure, processes, and functioning when altered by stressors like invasive species, climatic factors such as drought, and disturbances such as overgrazing by livestock and altered fire regimes (Holling 1973). (See Appendix 1 for definitions used in this report.) ***Resistant*** ecosystems have the capacity to ***retain*** their fundamental structure, processes, and functioning when exposed to stressors, disturbances, or invasive species (Folke 2004). Resistance to invasion by nonnative plants is increasingly important in sagebrush ecosystems; it is a function of the abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen 2004**)**. By identifying key indicators of the capacity of ecosystems and species to recover from disturbance and resist stressors like invasive plants, it is possible to assess and predict how they will respond to persistent threats and management actions over large planning areas.

Species are likely to be more resilient if connected populations exist in large blocks of high quality habitat across the full breadth of environmental conditions to which the species is adapted (Redford et al. 2011). Greater sage-grouse is a broadly distributed and wide ranging species that can move long distances between seasonal habitats (Connelly et al. 2011a,b; Fedy et al. 2012; Tack et al. 2011), and threat management necessarily requires a strategic, multi-scale approach that integrates both landscape prioritization and site-scale decision tools. Because of its widespread distribution and the broad range of sagebrush habitats that sage-grouse use, managers have considered GRSG an umbrella species for identifying ecological conditions required for a larger set of sagebrush-obligate species across large landscapes (Hanser and Knick 2011; Rowland et al. 2006). Holistic management approaches based on resilience science that address large-scale threats to GRSG and GUSG habitat should benefit sagebrush ecosystems and most sagebrush obligate species (see Evans et al. 2013).

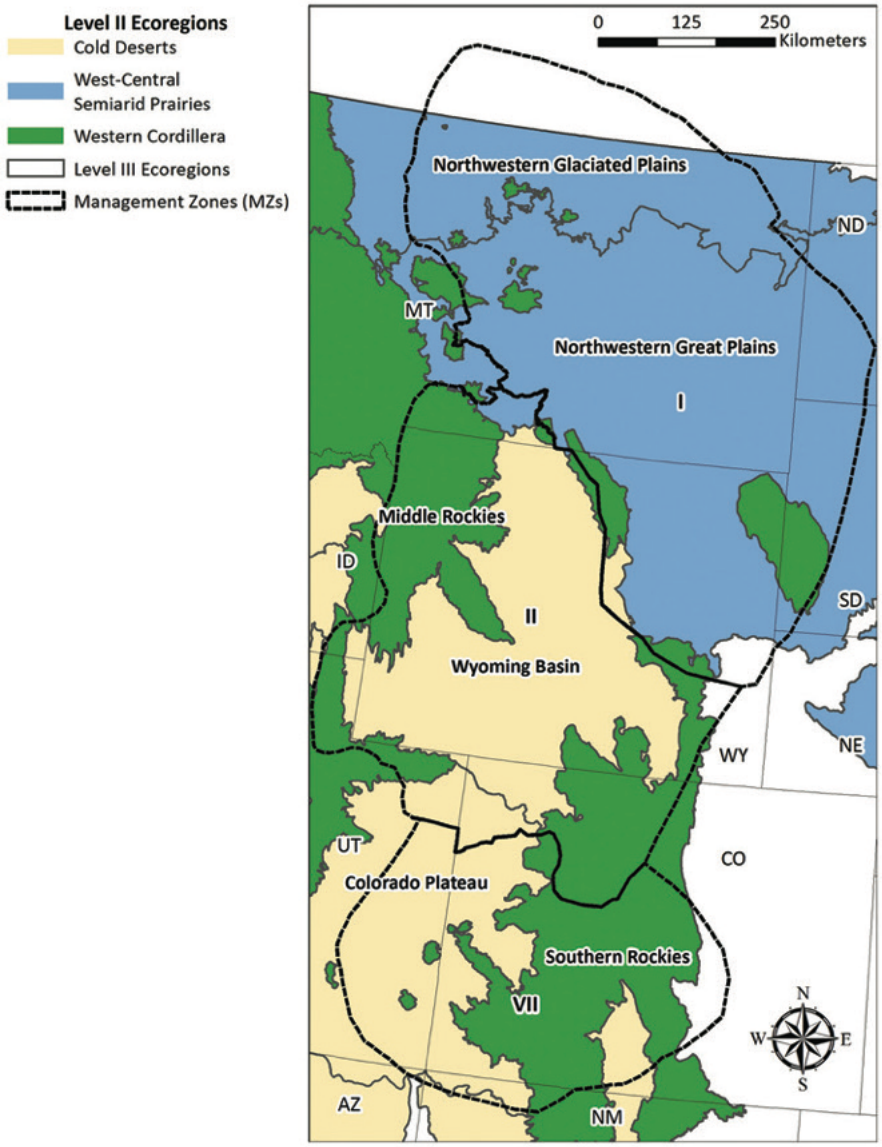
The use of resilience science has recently been fully operationalized for conservation of sagebrush ecosystems and GRSG in the Cold Desert ecoregions of the western portion of the GRSG range (Management Zones III, IV, and V; Chambers et al. 2014a). Here, we expand the approach that was developed to include the eastern portion of the range (Management Zones I, II, and VII identified in Stiver et al. 2006), which differs from western GRSG range in the magnitude of ecosystem versus land use and development threats and encompasses a different set of climatic regimes and vegetation types. We first discuss the climatic regimes and vegetation types that characterize the ecoregions in Management Zones I, II, and VII and review the primary threats to sagebrush ecosystems, GRSG, and GUSG in these ecoregions. We then discuss factors that determine ecosystem resilience to stressors and disturbances and resistance to nonnative invasive annual grasses in these ecoregions, and we provide an overview of the relative resilience and resistance of the predominant ecological types. We develop a sage-grouse habitat matrix in which we link the information that we developed on relative resilience to disturbance and resistance to nonnative invasive annual grasses with breeding habitat probabilities (Doherty et al. 2016) to both identify priority areas for management and determine effective management strategies at landscape scales. We also provide an

approach for targeting areas for habitat management that overlays Priority Areas for Conservation (USFWS 2013) for GRSG, critical habitat for GUSG (GSGRSC 2005, as updated; USFWS 2014a), and breeding bird population indices with resilience to disturbance and resistance to invasive annual grasses to spatially link sage-grouse populations with indicators of habitat conditions and risks. Finally, we review the tools and data available for assessing the suitability of targeted areas for treatment and determining the most appropriate management treatments. Throughout the report, we emphasize the importance of providing information that can help guide management and restoration strategies to maintain or enhance GRSG and GUSG habitat.

3. Climatic Regimes and Vegetation Types

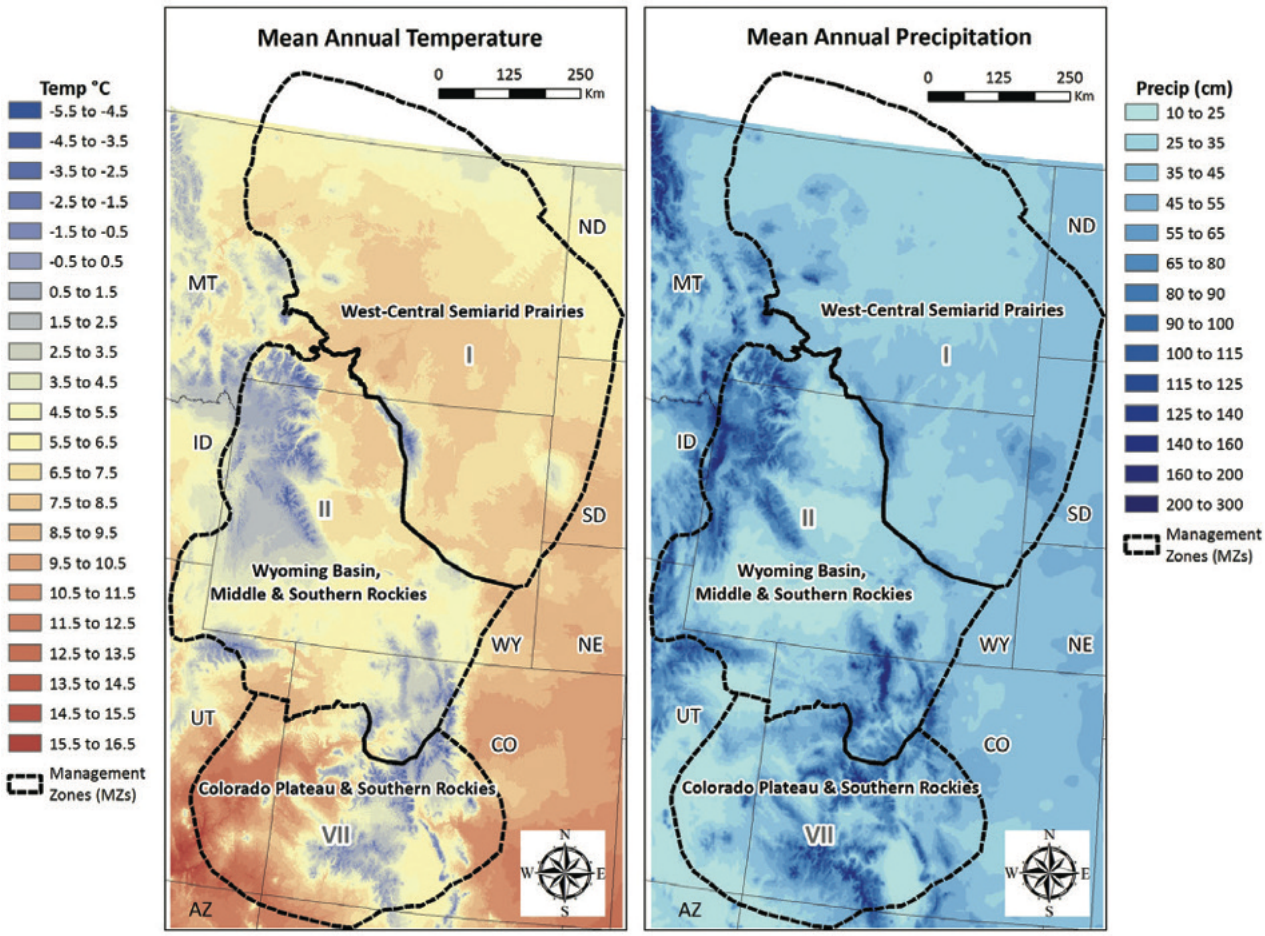
The eastern portion of GRSG range is characterized by different ecoregions that vary with respect to the type and extent of sagebrush habitat and persistent ecosystem threats. Here, we use Level II and Level III Environmental Protection Agency Ecoregions as the basis for describing these differences. The eastern portion of the range encompasses three Level II and six Level III ecoregions: the Cold Desert, which includes the Wyoming Basin and Colorado Plateau; West-Central Semiarid Prairies, which includes the Northwestern Glaciated Plains and Northwestern Great Plains; and Western Cordillera, which includes the Middle Rockies and Southern Rockies (fig. 1; Griffith 2010). Each of these ecoregions is characterized by distinct temperature and precipitation regimes (fig. 2) and differs in the amount of precipitation received in winter vs. summer (fig. 3). Greater sage-grouse Management Zones were based largely on these ecoregional differences, and the relationships between the two land classifications are shown in figure 1.

Differences in overlap between seasonality of precipitation and temperature, and onset of the dry season, are of particular importance in determining ecoregional differences. These differences, especially when coupled with amount of precipitation, influence both plant functional type dominance (Lauenroth et al. 2014; Sala et al. 1997) and competitive interactions with invasive species such as cheatgrass (*Bromus tectorum*) and field brome (*B. arvensis*, formerly *B. japonicus*) (Bradford and Lauenroth 2006). Amount of precipitation that is received during the period when temperature and potential evapotranspiration are low influences the amount of water stored in deep soil layers and therefore the balance between woody and herbaceous species (Lauenroth et al. 2014; Sala et al. 1997). Areas that receive more winter/spring precipitation typically have greater deep soil water storage and are dominated by woody species, such as sagebrush, which are more effective at using deep soil water (figs. 4a,b). In contrast, areas that receive predominantly summer precipitation are typically dominated by grasses. Also, seasonality of precipitation during the period when temperatures are favorable for plant growth is an important factor influencing the balance between C3 and C4 (cool and warm season) species with C3 species such as wheatgrasses (e.g., *Agropyron* and *Elymus* spp.) dominating in areas with cool, wet springs and C4 species such as grama grasses (*Bouteloua* spp.) dominating in areas with warm, wet summers (Paruelo and Lauenroth 1996; Sala et al. 1997). These differences are reflected in the land cover of sagebrush for the eastern portion of the range (figs. 5, 6).



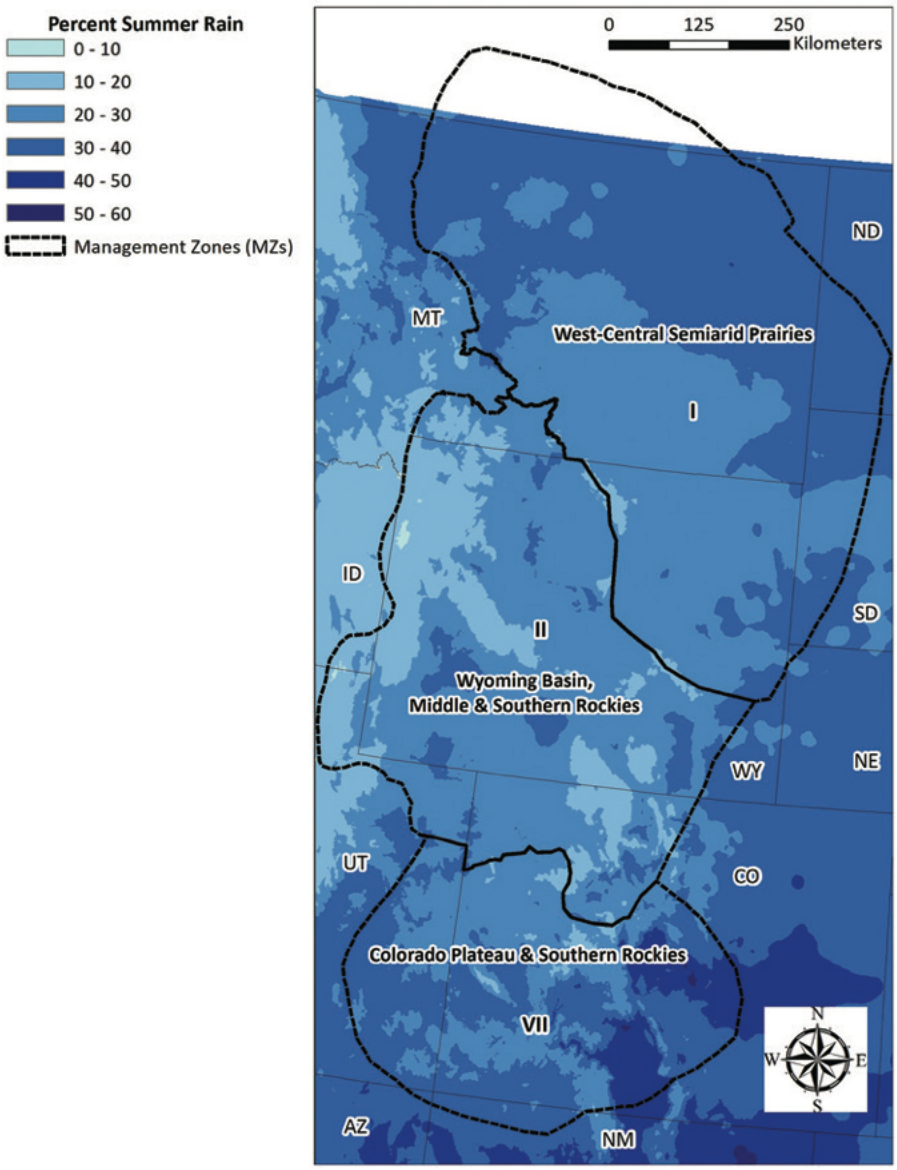
aLB(4 —The Level II and Level III Ecoregions (EPA 2016) occurring in Management Zones I, II, and VII (Stiver et al. 2006).

Resistance to *Bromus* species generally increases as summer precipitation and amount of precipitation increase (fig. 4c) as a function of increasing perennial grass productivity and dominance. This appears to be due to less favorable conditions for establishment of annual species like cheatgrass and strong competition from perennial native grass species that dominate under this precipitation regime (Bradford and Lauenroth 2006; Bradley 2009). However, even in this competitive environment, disturbances that remove perennial native grass cover often facilitate establishment of invasive annual grasses and other nonnative invasive plants (Bradford and Lauenroth 2006; Knight et al. 2014; Lauenroth et al. 2014).



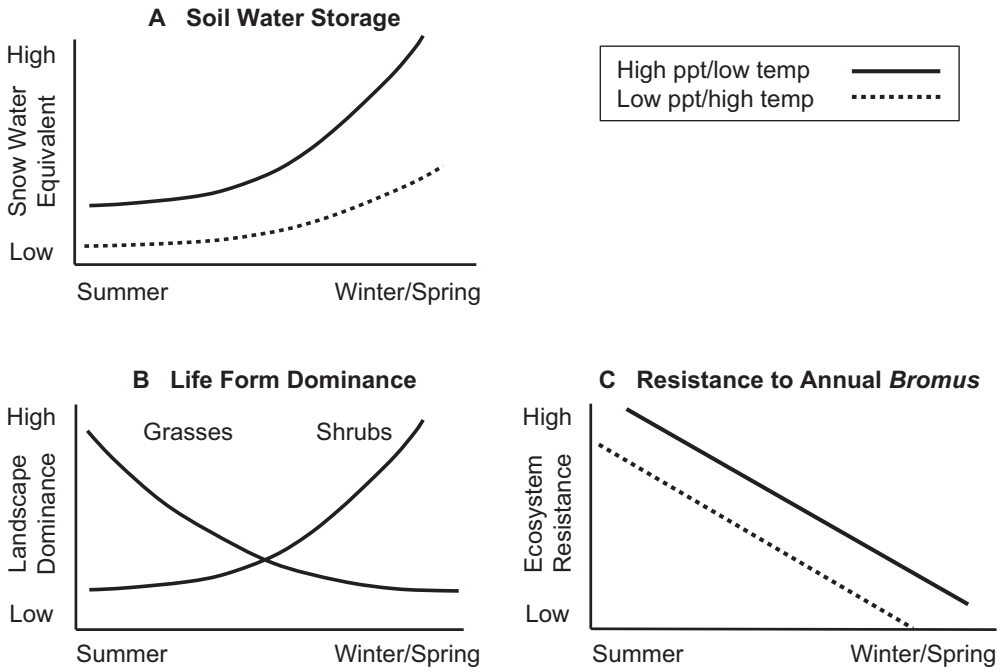
aURHNjE—The 30-yr normal annual values for precipitation and temperature (PRISM) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).

Soil climate regimes (temperature and moisture) integrate several different climate variables including mean annual temperature and precipitation and seasonality of precipitation thus providing a means of assessing climatic differences among ecoregions and effects on vegetation. These regimes are mapped as part of the National Cooperative Soil Survey (USDA NRCS 2016) and thus can be used in large-scale analyses (Maestas et al. 2016). (See Appendix 2 for an explanation of soil temperature and moisture regimes.) Also, they are a key component of Ecological Site Descriptions— part of a widely used land classification system that describes the potential of a set of climatic, topographic, and soil characteristics to support a dynamic set of plant communities and provide necessary information for determining the most appropriate management actions at site scales (Caudle et al. 2013; USDA NRCS 2015a). The soil temperature and moisture regimes that characterize sagebrush ecosystems in the eastern range vary due to the large latitudinal difference and elevation gradients that the area encompasses as well as the variation in seasonality of precipitation (fig. 7).



aLB(4 —Percentage of annual precipitation occurring during the months of July, August, and September (PRISM) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).

As with most large-scale mapping products, there are limitations in using Soil Survey information including incongruities in soil regime classifications, especially along mapping boundaries, and variation in the level of survey detail available. However, these areas represent a relatively minor component of the data set and have been taken into account in this report. Until improved products emerge, the Web Soil Survey (http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx) still provides the most complete data set to advance understanding of resilience and resistance concepts across the sagebrush biome. Project level planning can be informed by local climate and soils data.

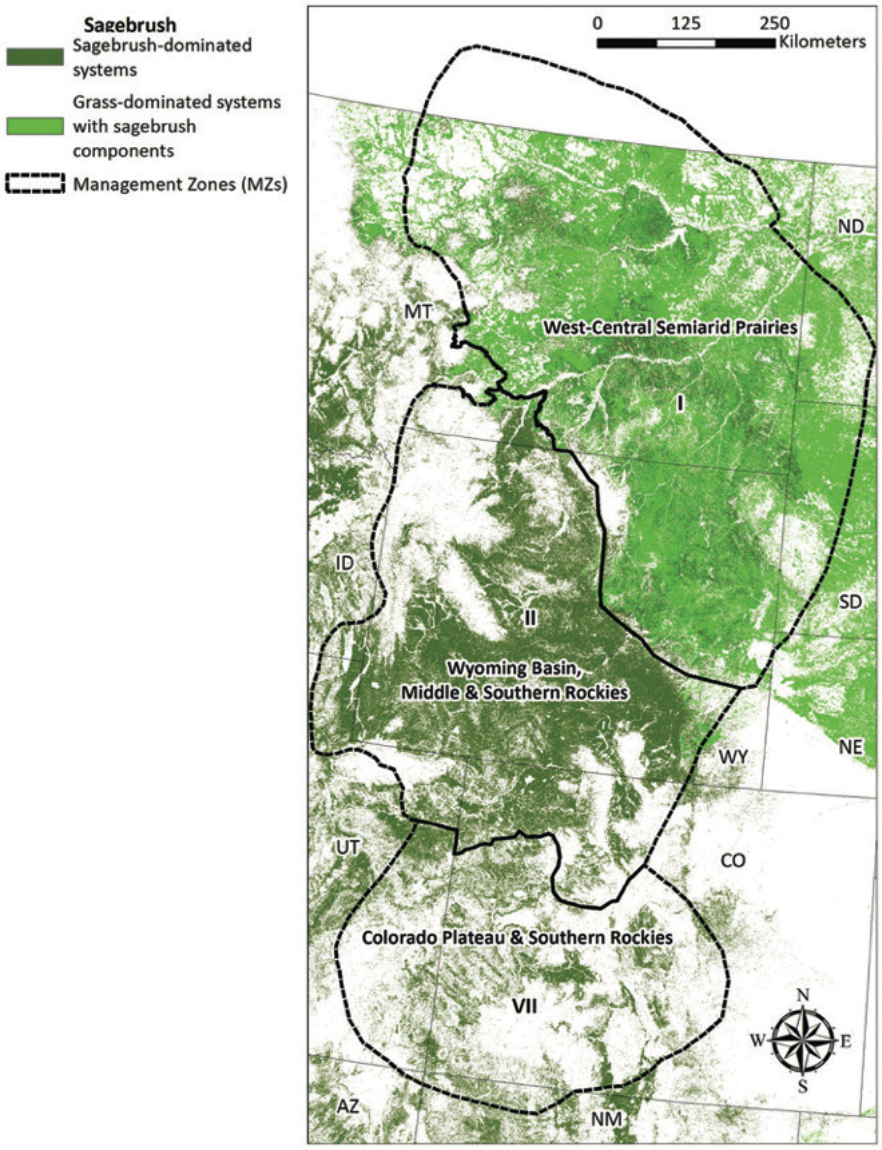


LH —Changes in soil water storage, life form dominance, and resistance to annual *Bromus* as seasonality of precipitation transitions from primarily summer to winter. **A.** Soil water storage increases as winter/spring precipitation and snow water equivalent increase and these changes are relatively greater for areas with relatively high precipitation and low temperature. **B.** Landscape dominance of grasses is highest with primarily summer precipitation; shrub dominance is greatest with primarily winter/spring precipitation. **C.** Resistance to *Bromus* is higher in areas where soil water storage is low and grasses dominate largely due to strong resource competition. Decreases in effective precipitation can increase resource fluctuations and lower resistance to *Bromus.* At more local scales, resistance also is influenced by nutrient availability and disturbance (based on Chambers et al. 2016a).

West-Central Semiarid Prairies is represented by the Northwestern Glaciated Plains in northern Montana and the Northwestern Great Plains in the west and central Dakotas, southeast Montana, and northeast Wyoming (Griffith 2010). The Northwestern Glaciated Plains are comprised of rolling hills and gentle plains mantled by glacial till, outwash, and glaciolacustrine sediments, while the Northwestern Great Plains were not glaciated and have rolling plains of shale and sandstone punctuated by occasional buttes.

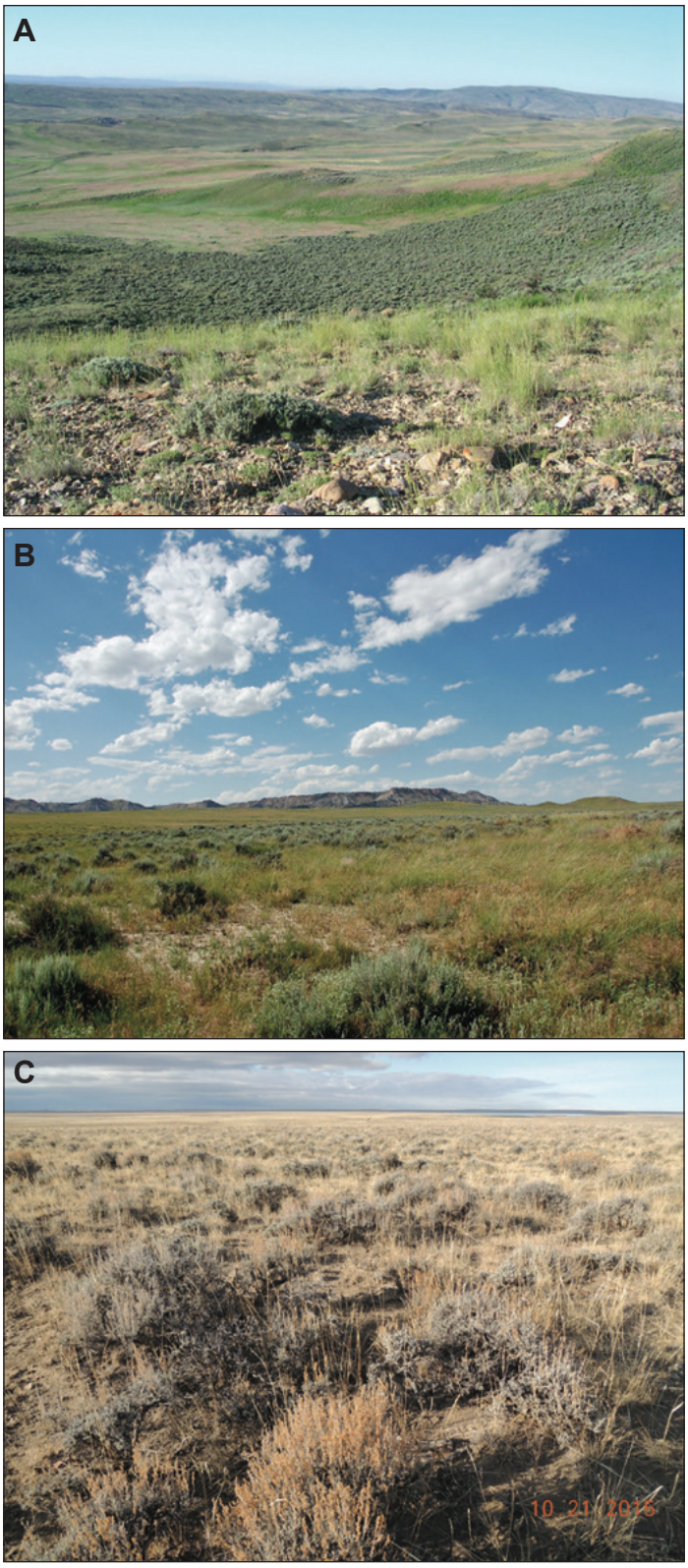
The West-Central Semiarid Prairie Ecoregion has a mostly dry, mid-latitude climate and is characterized by warm to hot summers and cold winters. Mean annual temperatures range from 37.4 °F to 47.3 °F (3 °C to 8.5 °C), while mean annual precipitation ranges from 9.8 inches to 21.6 inches (25 cm to 55 cm). In the Northwestern Glaciated Plains soil temperature and moisture regimes are predominantly cool (frigid) and summer moist (ustic), respectively, but in the Northwestern Great Plains both cool (frigid) and warm (mesic) soil temperature regimes and summer moist bordering on dry (ustic bordering on aridic) soil moisture regimes are typical.

Cook and Irwin (1992) evaluated vegetation characteristics along a west to east gradient at 14 study sites between Idaho and the Dakotas. They found that shrub cover diminished and graminoid cover increased at relatively constant rates across

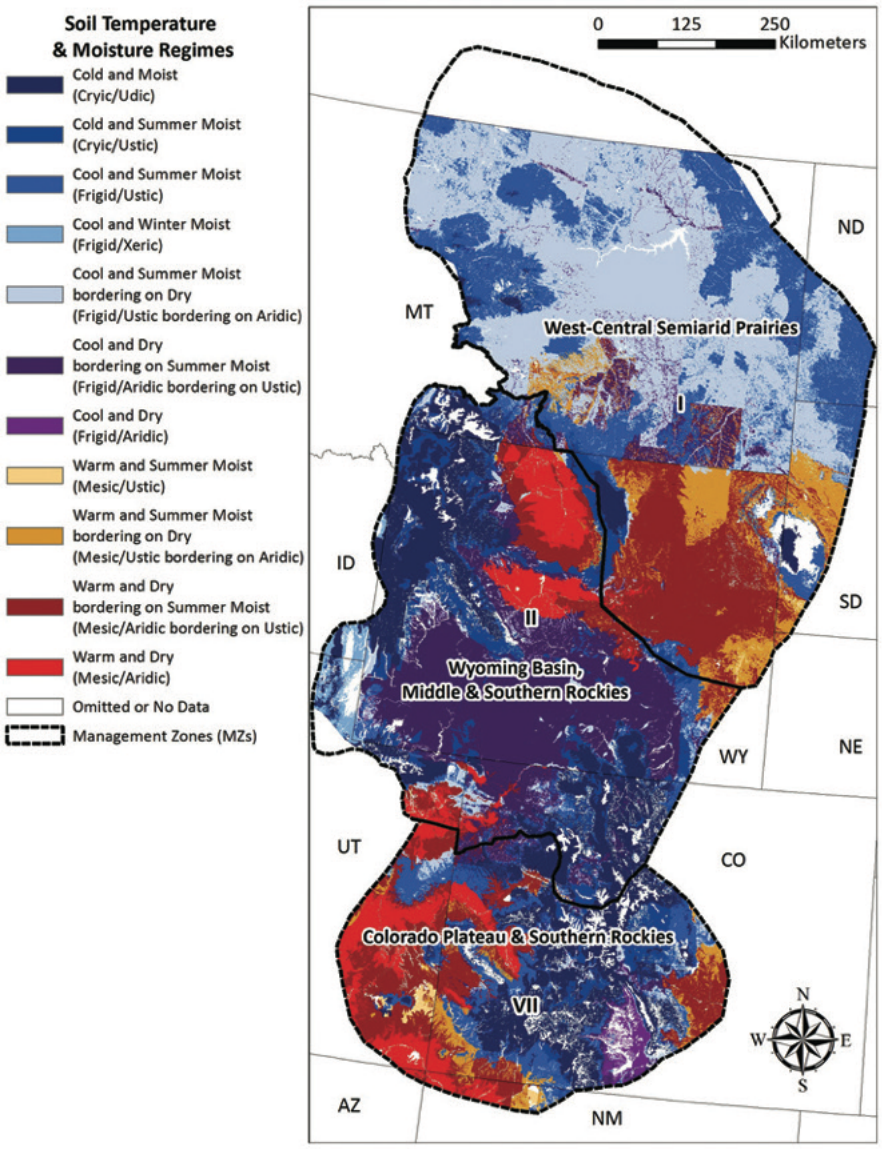


aLB(4 —Sagebrush-dominated ecological systems and grass-dominated ecological systems with sagebrush components (USGS 2014) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).

this west to east gradient. Graminoid cover was positively associated with increased summer precipitation, whereas shrub cover was positively correlated with winter precipitation. Thus, climate patterns of the eastern portion of the Northwestern Great Plains favor grassland communities. Sagebrush species include silver sagebrush (*A. cana* spp. *cana*), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*), fringed sagewort (*A. frigida*), and basin big sagebrush (*A. tridentata* ssp. *tridentata*) (Miller et al. 2011; USGS 2013). Dominant grasses include wheatgrasses (*Pascopyrum smithii* and *Elymus* spp.), grama grasses (*Bouteloua* spp.), bluestem species (*Andropogon gerardii, Schizachyrium scoparium*), and needlegrasses (*Hesperostipa spp., Nasella spp.*, and *Achnatherum spp.*), which vary widely in relative abundance in response to climate, drought conditions, and grazing pressure (Barker and Whitman 1988).



—Representative Wyoming big sagebrush ecological types in (A) the Powder River Basin in the West-Central Semiarid Prairies (Management Zone I) (photo by C. P. Kirol), (B) the Rochelle hills in eastern Wyoming (Management Zone I) (photo by C. Duchardt), and (C) the Wyoming Basin in the Cold Desert (Management Zone II) (NRCS file photo).



aURHNj□—Soil temperature and moisture regimes by soil moisture subclass in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). See Appendix 2 for an explanation of the soil temperature and moisture regime data used in this report. The area near the border between southeastern Montana and northeastern Wyoming is in a transition zone between the frigid and mesic soil temperature regimes, which has resulted in an apparent abrupt change in temperature regime at the State border. Future updates to soil survey information will resolve these join issues along political boundaries, using current climate datasets and additional field data.

The Cold Desert in the eastern part of the sage-grouse range includes the Wyoming Basin in the western and central portions of Wyoming, and the Colorado Plateau in eastern and southern Utah and western Colorado. The Wyoming Basin is a broad, intermontane basin that ranges in elevation from about 4,000 ft to 9,450 ft (1,220 m to 2,850 m) and is characterized by sedimentary landforms and variable topography, while the Colorado Plateau is deeply dissected tableland comprised of sedimentary rock that ranges from about 2,950 ft to over 9,840 ft (900 m to over 3,000 m).

The Cold Desert ecoregion in general has a continental climate with warm to hot and dry summers and cool to cold and wet winters. In the Wyoming Basin, mean annual temperature ranges from about 32 °F to 46.4 °F (0 °C to 8 °C) and mean annual precipitation ranges from 5.1 in to 19.7 in (13 cm to 50 cm). In the warmer Colorado Plateau, mean annual temperature ranges from approximately 41 °F (5 °C) at high elevations in the north to 59 °F (15 °C) in southern canyons, and mean annual precipitation ranges from 5.1 in (13 cm) at lower elevations in the south to more than 31.5 in (80 cm) at high elevations. Cool and warm (frigid and mesic) soil temperature regimes and dry and summer moist (aridic and ustic) soil moisture regimes occur in the Cold Desert ecoregion.

Vegetation is characterized largely by arid to semiarid shrublands that transition from zero to a few warm season grasses west of the Continental Divide, to warm season grasses as a major component east of the Continental Divide (Griffith 2010). Lower elevation sagebrush types are dominated by Wyoming big sagebrush. Black sagebrush (*A. nova*) occurs on windswept ridges and in areas with shallow soils while early sagebrush (*A. arbuscular* ssp. *longiloba*) occurs on sites with higher precipitation and clay content. Basin big sagebrush (*A. tridentata* ssp. *tridentata*) is found in areas with deeper soils and higher available soil moisture across the region, as is silver sagebrush in eastern portions of the Wyoming Basin. In ecotones between Cold Desert and Western Cordillera Ecoregions at mid elevations, Wyoming big sagebrush transitions into mountain big sagebrush, and at higher elevations mountain big sagebrush co-occurs with mountain shrubs (e.g., Saskatoon serviceberry [*Amelanchier alnifolia*], antelope bitterbrush [*Purshia tridentata*], and snowberry [*Symphoricarpos* spp.]). In these zones in Colorado, extensive areas of hybridization occur between black sagebrush and mountain big sagebrush, and between Wyoming big sagebrush and mountain big sagebrush (Monsen 2005; Winward 2004). Bunchgrasses are common and include wheatgrasses, needlegrasses, fescues (*Festuca* spp.), and bluegrasses (*Poa* spp.).

Utah juniper (*Juniperus osteosperma*) occurs in the more arid basins in the western part of the ecoregion, while Rocky Mountain juniper (*J. scopulorum*) is common at higher elevations and in the east where summer precipitation is higher. In the Colorado Plateau, two-needle piñon (*Pinus edulis*) co-mingles with Utah juniper.

The Western Cordillera is represented by the Middle Rockies (which occur in southwestern Montana, eastern Idaho, western Wyoming, the Black Hills of western South Dakota and northeastern Wyoming) and the Southern Rockies (which extend from southern Wyoming through Colorado) (Griffith 2010). The Western Cordillera Ecoregion is characterized by high elevation mountains and foothills that range from 5,085 ft to over 14,400 ft (1,550 m to over 4,390 m), and by cool to warm short summers and cold winters.

Mean annual temperature and precipitation vary greatly with elevation. In the Middle Rockies, mean annual temperatures range from approximately 23 °F to 46.4 °F (–5 °C to 8 °C) and precipitation ranges from 11.8 in (30 cm) to over 98.4 in (250 cm). Soil temperature regimes are cool to cold (frigid to cryic), and soil moisture regimes are summer moist and wet and humid (ustic and udic). In the Southern Rockies, mean annual temperatures range from about 24.8 °F to 51.8 °F (–4 °C to 11 °C), and precipitation ranges from 9.8 in (25 cm) to over 68.9 in (175 cm). Soil temperature regimes range from warm to cold (mesic to cryic), and moisture regimes range from dry to wet and humid (aridic to udic).

Dominant sagebrush species at higher elevations are mountain big sagebrush, low sagebrush (*A. arbuscula*), silver sagebrush, three-tip sage (*A. tripartita*), and spiked big sage (*A. tridentata* ssp. *spiciformis*), and at lower elevations are Wyoming big sagebrush and black sagebrush (Knight et al. 2014). Utah juniper and two-needle piñon occur in the lower and more arid areas in the western and southern part of the ecoregion, while Rocky Mountain juniper is common at higher elevations. The Middle Rockies and Southern Rockies are characterized by many of the same grass species as the Cold Desert ecoregions (fig. 1) including wheatgrasses, needlegrasses, fescues, and bluegrasses.

Grouse, and Gunnison Sage-Grouse

The relative importance of persistent ecosystem threats versus land use and development threats for GRSG was summarized in the Sage-Grouse Conservation Objectives Final Report (COT Report; USFWS 2013) based on known occurrence of threats, existing management strategies, and professional experience. Threats to GUSG are summarized in the Gunnison Sage-grouse Rangewide Conservation Plan (GSGRSC 2005) and the final U.S. Fish and Wildlife Service listing decision (2014a). Here we discuss these threats for the GRSG habitat in the eastern portion of the range and for GUSG habitat range-wide to inform a resilience and resistance approach. We focus on the effects of persistent ecosystem threats and the secondary ecosystem threats of land use and development. Because the Cold Desert transitions into the Western Cordillera and have similar threats, we combine them for this discussion.

Persistent Ecosystem Threats

West-Central Semiarid Prairies (Management Zone I)

Herbivory, in conjunction with fire, has significantly influenced plant community composition, structure, and production of plant communities in the West-Central Semiarid Prairies (Knapp 1996). Historically, large numbers of bison (*Bos bison*) moved nomadically through the area in response to changes in vegetation associated with drought, past herbivory, and fire (Bragg and Steuter 1996). Grazing by bison occurred across large areas as huge herds moved through, and the impacts of these herds on the vegetation, soils, and riparian areas were probably extensive. The interval between grazing episodes may have ranged from 1 to 8 years (Malainey and Sherriff 1996). Knopf (1996) suggests that the mixed and short-grass prairies comprising the West-Central Semiarid Prairies supported not only a significant portion of the North American bison population, but also the highest densities of black-tailed prairie dogs (*Cynomys ludovicianus*). Rocky Mountain locusts (*Melanoplus spretus*), which became functionally extinct by 1900, often erupted in swarms numbering in the billions and their impact on vegetation was also presumed to be extensive (Lockwood and DeBrey 1990). Managed domestic livestock grazing (mostly cattle) has largely replaced these herbivores across the landscape and their impacts on grassland habitats are different in scale and duration.

Drought also played an important role in the composition of plant communities in this ecoregion, and it resulted in temporal changes in the dominant graminoid

species (e.g., shifts from western wheatgrass to blue grama; Bragg and Steuter 1996). Large fires often occurred, but fire regimes were probably highly variable depending on rainfall and subsequent grass growth (Umbanhowar 1996). The burns removed much of the vegetation, which resulted in continual shifts in the abundance and distribution of herbivores across large areas. In turn, drought and grazing by bison and/or locusts mediated the direction and extent of vegetation response (Umbanhowar 1996).

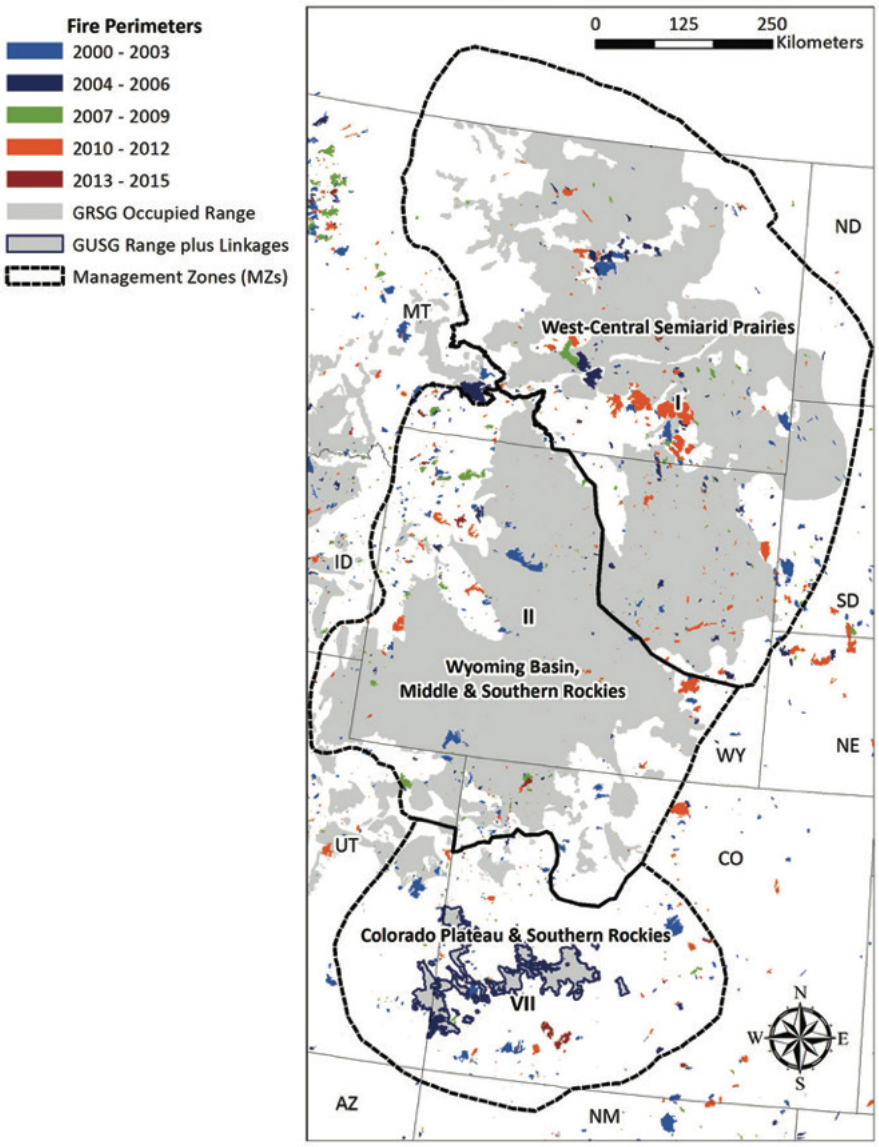
Euro-American settlement had profound impacts on this ecoregion. Prior to settlement, fire likely limited expansion of shrub communities, including sagebrush and, along with herbivory, fire was considered a significant disturbance in the West-Central Semiarid Prairies. Anthropogenic changes in landscape patterns resulting from Euro-American settlement reduced the extent and distribution of fires and likely resulted in increased shrub abundance. Numerous fires have burned in this ecoregion in the past 15 years, but most large fires have occurred within conifer dominated ecosystems and outside of sage-grouse Priority Areas for Conservation (fig. 8).

After Euro-American settlement, bison were removed from the landscape and a high proportion of the area was converted from native prairie to cropland (tilled agriculture). Much of this development occurred on sites with more productive (resilient) soils and temperature regimes. These areas were the breeding habitat for the Rocky Mountain locust, and conversion to cropland was presumably a primary driver of their extinction (Lockwood and Debrey 1990).

A number of homestead claims were filed on lands that were not suitable for non-irrigated agricultural development. Following the severe drought ("dust-bowl") years of the 1930s, portions of the area with a high number of failed homesteads were reacquired by the Federal government under the Bankhead Jones Farm Tenant Act (1937, as amended). The Bankhead Jones Act included provisions for development of a land conservation and utilization program. Land considered submarginal for cropland was purchased, rehabilitated, and used for purposes for which it was better suited (Maddox 1937).

Under management of the U.S. Department of Agriculture, conservation measures were taken to restore water and soil resources that included planting non-native grass species. Several introduced seeded species became widely naturalized, including crested wheatgrass (*Agropyron cristatum*) (Lesica et al. 1996). More recently, sweet clover (*Melilotus officinalis*), Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), timothy (*Phleum pratense*), annual bromes, and leafy spurge (*Euphorbia esula*) have altered native communities. Land use and development uses as well as climate change in this ecoregion may exacerbate effects of these species on sagebrush communities

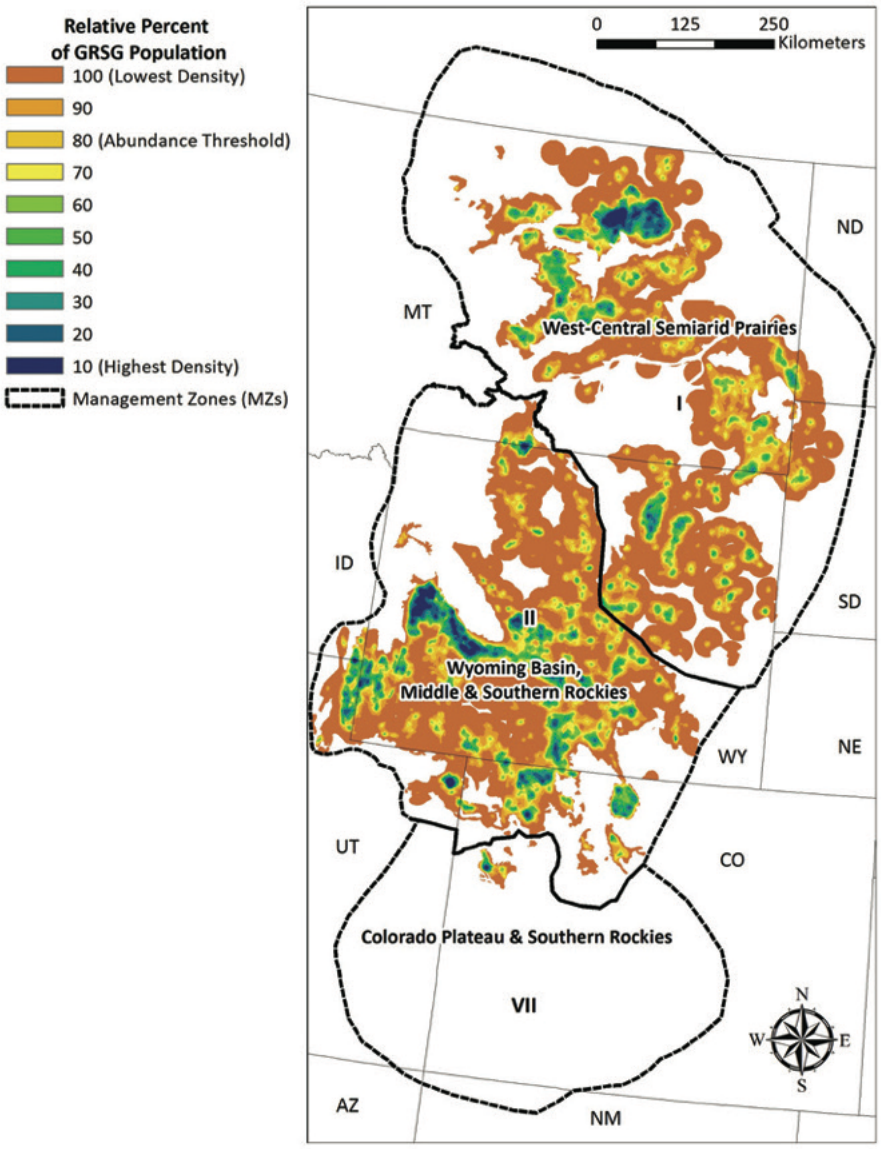
The West-Central Semiarid Prairies align with Management Zone I and in a recent analysis included 12.4 percent of the total GRSG population based on lek counts from 2010 to 2014 (fig. 9; Doherty et al. 2016). In this analysis, variables showing the highest importance for predicting breeding habitat were: tree canopy cover (negatively associated), cover of all sagebrush species (positively associated), terrain roughness (quadratic relationship), topographic wetness (quadratic relationship), and gross primary productivity (quadratic relationship) (table 1; see Doherty et al. 2016). This analysis clearly showed the overarching importance of environmental variables in determining suitable GRSG habitat. Greater sage-grouse habitats in Management Zone I are characterized by patchy and often sparse sagebrush



aURHNj□—Perimeters of fires that have occurred since 2000 in Management Zones I, II, and VII (Stiver et al. 2006), the Gunnison sage-grouse critical range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a), and associated ecoregions (EPA 2016). Data for fires >1,000 acres are from MTBS (2014) and data for fires <1,000 acres are from GeoMAC (2015).

cover, and just 14 percent of the landscape is classified as sagebrush compared to 45 percent in Management Zone II (fig. 5; Knick 2011). Within this patchwork of sagebrush, sage-grouse select areas that contain high cover of sagebrush to winter and nest (Doherty et al. 2008, 2010a; Herman-Brunson et al. 2009; Moynahan et al. 2006; Swanson et al. 2013).

In the COT Report (USFWS 2013), persistent and widespread threats in the West-Central Semiarid Prairies (Management Zone I) included weeds and annual grasses in the Yellowstone Watershed and Powder River Basin, and fire in North and South Dakota. Conifers were a localized threat in parts of the region. Land use and development activities including cropland conversion in the Yellowstone Watershed that eliminates sagebrush cover, and energy development throughout the ecoregion,



aURHNj□—Relative percentage of the Greater sage-grouse population based on breeding bird abundance during 2010 to 2014 (Doherty et al. 2016) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). Population index values were calculated separately for each management zone. Population bins are additive.

were considered significant threats. Understanding the relative effects of invasive species, fire, and conifer expansion across the ecoregion can help in determining the most effective management and restoration strategies in areas being affected by land use and development activities as well as in relatively intact areas.

Cold Desert and Western Cordillera Ecoregions (Management Zones II and VII)

Euro-American arrival in the mid-1800s initiated a series of changes in vegetation composition and structure in the Cold Desert that had cumulative effects on sagebrush habitats. First, improper grazing by livestock led to a decrease in native perennial grasses and forbs (Miller and Eddleman 2001; Miller et al. 2011).

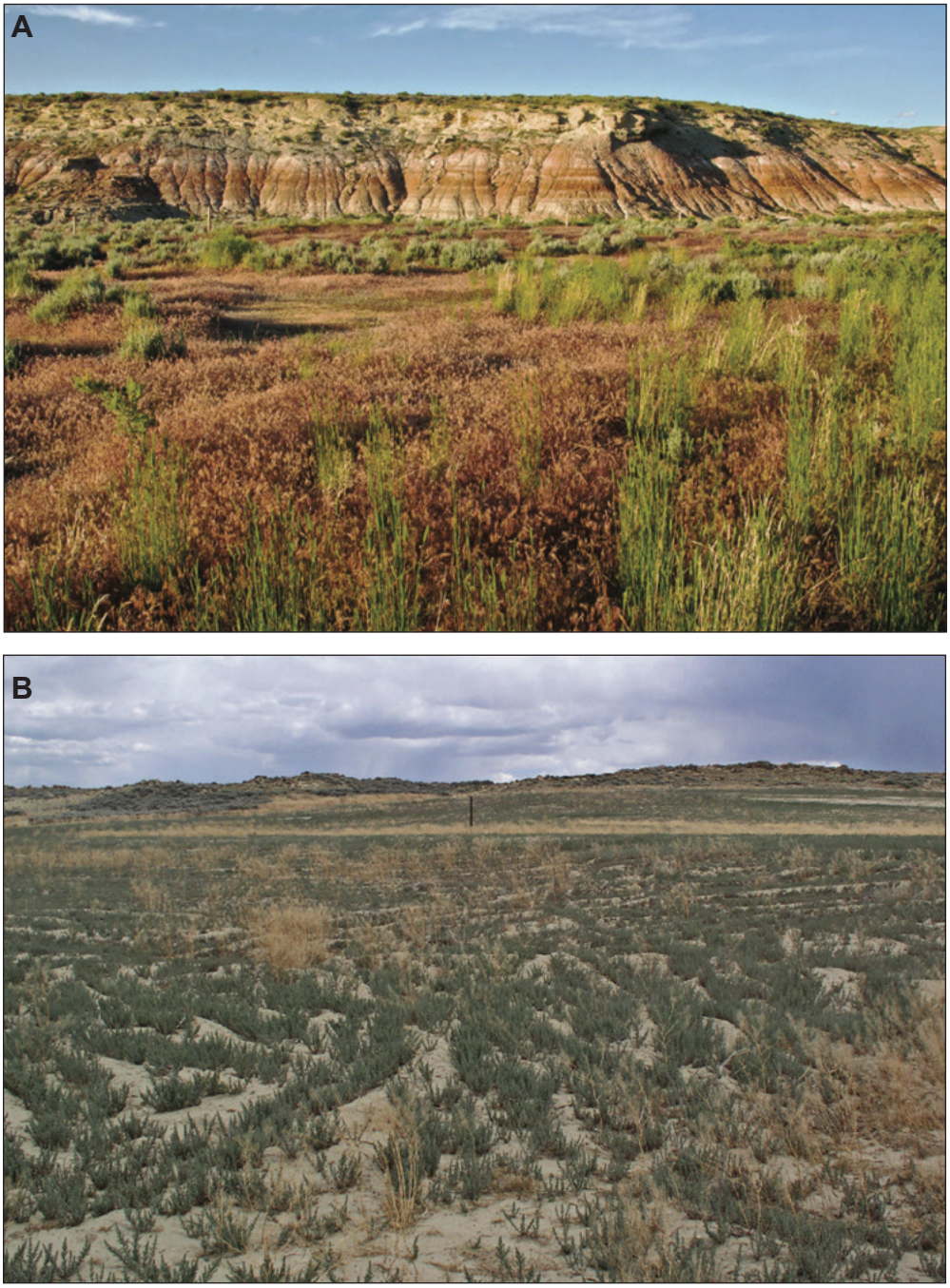
Table 1—Top predictor variables and relative importance values from Random Forest models for each Management Zone from Greater sage-grouse results (2010 to 2014) from Doherty et al. (2016) and Gunnison sage-grouse results (1995 to 2015) developed for this report.

f5W5B□H□Wl□ **zone**	aL□4wl□ **variable**	F□,PWJ□ **variable**	GkL4J□ **variable**	aP(4lk□ **variable**	aL□lk□ **variable**
I	Conifer cover	All sagebrush	Roughness	Topographic wetness	Gross primary production
Importance	1.00	0.63	0.57	0.55	0.45
II	All sagebrush	Conifer cover	Annual drought index	Degree days >5 °C	Mean annual precipitation
Importance	1.00	0.73	0.68	0.59	0.49
VII (Greater sage-grouse)	All sagebrush	Low sagebrush index	Human disturbance	Oil and gas wells	
Importance	1.00	0.67	0.48	0.4	
VII (Gunnison sage-grouse)	All sagebrush (4.0 km)	All sagebrush (0.56 km)	Conifer cover (0.56 km)	Annual drought index	Conifer cover (4.0 km)
Importance	1.00	0.64	0.53	0.39	0.32

Decreased competition from perennial herbaceous species, in combination with ongoing climate change and favorable conditions for woody species establishment at the beginning of the 20th century, resulted in a widespread increase in shrub abundance (primarily *Artemisia* species) and at mid elevations more localized increases in Utah and Rocky Mountain juniper and two-needle piñon pine (Baker 2011; Miller et al. 2011; Romme et al. 2009).

Second, invasive annual grasses (e.g., cheatgrass and field brome) were introduced from Eurasia in the late 1800s and spread into low to mid-elevation ecosystems that had depleted understories due to improper grazing or were disturbed by land development (Mealor et al. 2013; Knight et al. 2014). These grasses spread with wildfire disturbance in both the Wyoming Basin (Knight et al. 2014) and western Colorado Plateau (Floyd et al. 2006). Annual grass/fire cycles and increases in fire frequency are not yet as problematic as in the Great Basin and western portion of the range, but conversion to invasive annual grasses is an increasing problem in some areas (Baker 2011; Brooks et al. 2015; Mealor et al. 2012). On sites with oil and gas drilling and mining disturbances, invasive annual grasses and a host of other annual invaders typically increase at the expense of native species diversity and cover (fig. 10; Allen and Knight 1984; Bergquist et al. 2007). Also, vegetation management treatments designed to reduce Wyoming big sagebrush density and increase understory grasses and forbs often result in an increase in invasive annuals if already present (Beck et al. 2012). This leads to slow recovery of sagebrush canopy cover and height required by nesting and brooding sage-grouse (Hess and Beck 2012a).

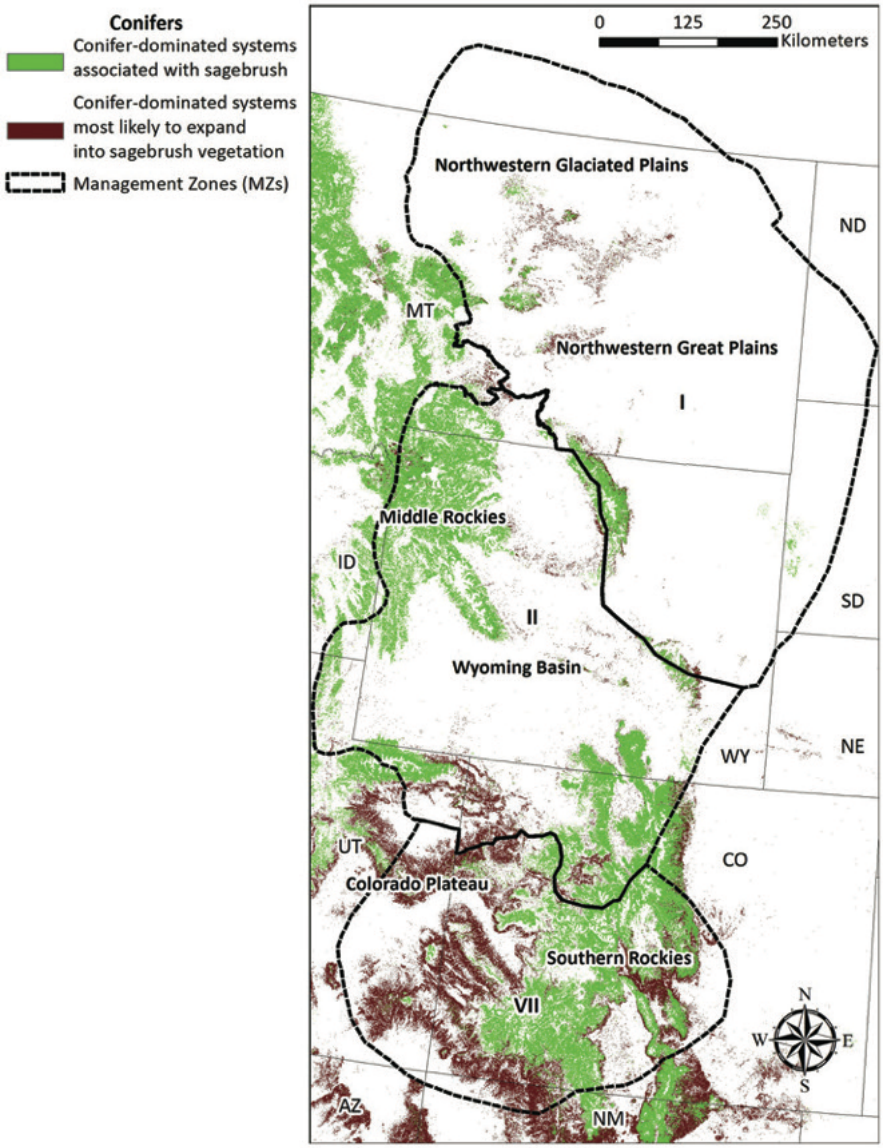
Third, expansion of juniper and piñon pine trees into sagebrush types at mid- to high elevations is occurring locally and is reducing the grass, forb, and shrub species associated with these types (fig. 11, 12; Romme et al. 2009). For example, infill of persistent woodlands and wooded shrublands and expansion of piñon and juniper into shrublands is occurring on portions of the Uncompahgre Plateau and Mesa Verde in southwestern Colorado (Eisenhart 2004; Floyd et al. 2004, 2006; Shinneman and Baker 2009). Infilling of trees increases woody fuels but reduces fine fuels that can result in less frequent fires than occurred historically in sagebrush dominated ecosystems (Miller et al. 2013). Fires in piñon and juniper stands at or



—Annual invasive species established on disturbed sites in Wyoming: (A) cheatgrass (*Bromus tectorum*) and (B) saltlover (*Halogeton glomeratatus*) (photos by K. Henke).

near full tree stocking are typically high severity (Baker and Shinneman 2004) and consequently result in significant losses of above- and below-ground organic matter with detrimental ecosystem effects (Miller et al. 2013).

Warmer temperatures and prolonged droughts may be increasing the risk of wildfire and invasive annual grasses in many of these ecosystems (Littell et al. 2009). Multiple fires have burned in Management Zones II and VII since 2000, often with uncharacteristically large sizes and severity (fig. 8). Although not within GUSG range, in southwestern Colorado in Mesa Verde National Park, a greater proportion of the piñon-juniper woodland burned in the decade between 1995 and 2005 than had burned throughout the previous 200 years (Floyd et al. 2006). Those stands that had sparse understories prior to burning are now dominated largely by cheatgrass and other annual invaders (Floyd et al. 2006).



aURHNj□—Conifer-dominated ecological systems (USGS 2014) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). The dark brown colors represent conifer-dominated systems most likely to expand into sagebrush-dominated systems (USDI BLM 2014), and are not intended to indicate areas with ongoing conifer expansion.



aURHNj□—Conifer expansion in the Big Horn Basin of the Cold Desert (Management Zone II) (photo by T. Christiansen).

In the COT Report (USFWS 2013), persistent ecosystem threats to GRSG were ranked high for much of the Wyoming Basin and Middle Rockies (Management Zone II). Fire was considered a persistent and widespread threat in six of the nine populations (North Park, Colorado; Northwest, Colorado; Middle Park, Colorado; Laramie, Wyoming; Rich-Morgan Summit, Wyoming and Utah; Uintah, Utah) and a localized threat in the remaining three (Eagle-South Routt, Colorado; Jackson Hole, Wyoming; Wyoming Basin, Wyoming) (fig. 8). Weeds and annual grasses were a persistent and widespread threat in eight populations and a low-ranked threat in one (Wyoming Basin, Wyoming). Conifers were a persistent and widespread threat in the Laramie and two Utah populations (Rich-Morgan-Summit and Uintah), and a localized threat in the remaining populations, except for Middle Park and North Park, Colorado, where conifers were not considered a threat (fig. 11).

In Doherty et al.'s (2016) analysis, Management Zone II included 36.8 percent of the range-wide total of male GRSG attending leks from 2010 to 2014 (fig. 9). Variables showing the highest importance for predicting breeding habitat were: cover of all sagebrush species (positively associated), tree canopy cover (negatively associated), annual drought index (quadratic relationship), degree days greater than 5 ^{o}C (quadratic relationship), and mean annual precipitation (quadratic relationship) (table 1; see Doherty et al. 2016). Similar to Management Zone I, these variables indicate the importance of environmental variables to sage-grouse habitats. Habitats in Management Zone II are characterized by broad expanses of sagebrush ecosystems, which provide resources for all life history needs of GRSG (Doherty et al. 2016; Fedy et al. 2014; Kirol et al. 2015a; Smith et al. 2014). Lek sites are an important predictor of GRSG populations, with approximately 95 percent of nests within 10 km from lek capture (Doherty et al. 2010a; Holloran and Anderson 2005).

In addition, individual GRSG from many populations in Management Zone II migrate between seasonal sagebrush habitats (Fedy et al. 2014).

Studies on the impacts of conifer expansion on GRSG and GUSG from across the eastern portion of the range indicate both species avoid or are negatively associated with conifer cover during lekking and nesting as well as during summer and winter (Aldridge et al. 2012; Doherty et al. 2008, 2016; Fedy et al. 2014; Walker et al. 2016). But Kirol et al. (2015a) reported a positive response for non-brooding female GRSG in summer in south-central Wyoming. Furthermore, summer survival of females in Wyoming was negatively associated with proximity to forested areas (deciduous and conifer stands), where on average, GRSG mortality was higher closer to woodlands than for locations farther from woodlands (Dinkins et al. 2014b). In the Gunnison Basin, GUSG also selected nest sites farther from conifer (including juniper) cover, and nesting habitat quality was lower within 350 m of forested habitat (Aldridge et al. 2012). A doubling of GUSG males occurred on three leks in southwestern Colorado 2 to 3 years after piñon-juniper reduction near the leks (Commons et al. 1999). Outside the eastern region, GRSG have been shown to incur population-level impacts at a very low level of conifer expansion and the likelihood of maintaining breeding activity is severely compromised when conifer canopy exceeds 4 percent in the immediate vicinity of the lek (Baruch-Mordo et al. 2013).

Persistent ecosystem threats coupled with land use and development threats can exacerbate potential impacts to sage-grouse. For example, environmental conditions such as sagebrush cover and availability of riparian areas interact with other stressors including land use and development and predatory birds such as *Buteo* hawks, common ravens (*Corvus corax*), and golden eagles (*Aquila chrysaetos*) in Management Zone II (Dinkins et al. 2012, 2014a). In turn, these stressors influence survival rates for GRSG (Dinkins et al. 2014b; Kirol et al. 2015b; LeBeau et al. 2014).

Also, increasing land use and development in the Wyoming Basins fragments habitat and promotes establishment of invasive species such as cheatgrass, which may lead to increasing wildfire (Hess and Beck 2012b). Numbers of oil and gas well pads, percent area of wildfire, and variability of shrub height within 1 km of leks were all correlated with GRSG lek abandonment in the Bighorn Basin of north-central Wyoming (Hess and Beck 2012b). These additive factors, all related to increasing disturbance, were reported to be connected to reduction in habitat quality, partly related to establishment and spread of cheatgrass and increasing wildfire (Hess and Beck 2012b). Although annual grasses do not yet dominate GRSG habitats in the Wyoming Basin, results from a microhabitat selection study in the south-central portion of this region indicate female sage-grouse nest site selection was negatively correlated with presence of cheatgrass and positively with canopy cover of mountain and Wyoming big sagebrush (Kirol et al. 2012).

In the COT Report (USFWS 2013), persistent ecosystem threats varied in importance for GRSG populations in the Colorado Plateau and Southern Rockies (Management Zone VII). Fire was a persistent and widespread threat in both populations (Parachute-Piceance-Roan Basin and Meeker-White River, Colorado) (fig. 8), weeds and annual grasses were a localized threat in both populations (fig. 10), and conifers were a persistent and widespread threat in the Parachute-Piceance-Roan Basin, Colorado, population and not a threat in the Meeker-White River, Colorado, population (fig. 11).

In Doherty et al.'s (2016) analysis, Management Zone VII included 0.3 percent of the rangewide total of GRSG males on leks from 2010 to 2014 (fig. 9). The four variables important for predicting breeding habitat of these small populations were: cover of all sagebrush species (positively associated), cover of low sagebrush (positively associated), human disturbance index (negatively associated), and oil and gas wells (negatively associated) (table 1; see Doherty et al. 2016).

The Colorado Plateau and adjacent Southern Rockies (Management Zone VII) encompass the entire population of GUSG, which was estimated at 4,700 birds rangewide in 2014 (fig. 13; USFWS 2014a). About 85 percent of the entire population of GUSG occurs in the Gunnison Basin while the remaining birds occur in six satellite populations in southwestern Colorado and southeastern Utah.

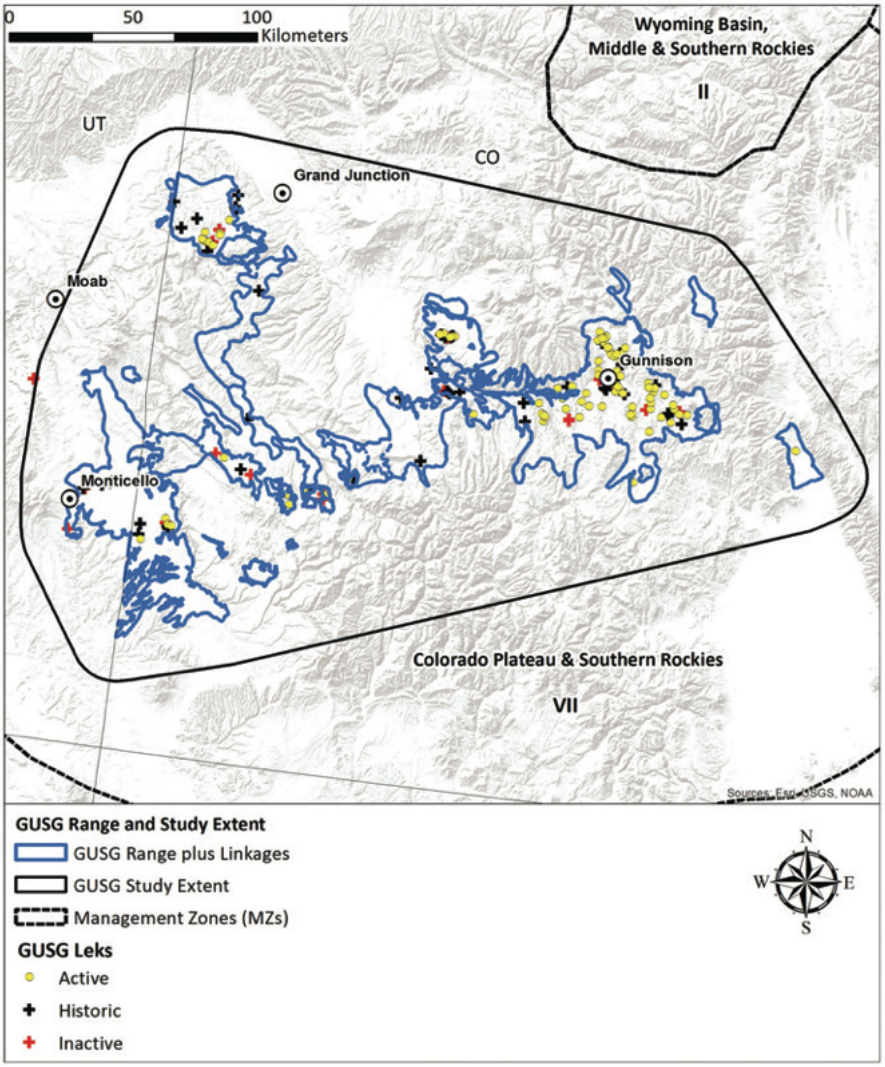
Invasive plants, piñon and juniper expansion, and wildfire are considered to be secondary and/or localized threats to GUSG. Some GUSG habitat has been affected by invasive plants, especially cheatgrass, but the impacts do not currently appear to be threatening individual populations or the species rangewide (GSGRSC 2005; USFWS 2014a). However, invasive plants continue to expand their range, facilitated by ground disturbances such as wildfire, grazing, and human infrastructure. Climate change will likely alter the range of individual invasive species, accelerating the decline of sagebrush communities (USFWS 2014a). Drought impacts are already considered a high to very high level of threat in two satellite populations (San Miguel, Colorado and Dove Creek/Monticello, Utah and Colorado; GSGRSC 2005). Most populations are experiencing low to moderate levels of piñon-juniper expansion although piñon-juniper expansion has been considerable in the Crawford and Piñon Mesa populations (GSGRCS 2005; USFWS 2104a).

The models developed for this report indicate that the five variables important for predicting breeding habitat of the GUSG populations were: cover of all sagebrush species at the 4.0 km scale (positively associated); conifer cover (negatively associated) at both the 0.56 km and 4.0 km scales; cover of all sagebrush species at the 0.56 km scale (positively associated); and annual drought index (quadratic relationship) (table 1).

f?UCZ6jrSZVRj

Climate change projections and the likely effects of global warming differ among ecoregions in the eastern portion of GRSG range (U.S. National Climate Assessment, Kunkel et al. 2013a,b). In the Western Great Plains as a whole, average temperatures have increased throughout the region in the last few decades, with the largest changes occurring in winter months (Kunkel et al. 2013a). Also, the number of frost-free days has increased (Kunkel et al. 2013a). There have been no significant trends in precipitation, but there has been a significant increase in extreme precipitation events.

Future temperature projections are based on Global Circulation Models and depend on the models used, the carbon dioxide emissions scenario, and the time frame. Downscaled models are rare for the eastern portion of the range, but temperature values are generally similar for ensemble Global Circulation Models (CMIP3) with a reference period of 1980 to 2000 for the Great Plains and the Southwest United States (Kunkel et al. 2013a,b). Warming projections for low (B1) and high emissions (A2), respectively, range from 2.5 °F to 3.0 °F (4.5 °C to 5.4 °C) for 2035, 3.5 °F to 5.0 °F (6.3 °C to 9 °C) for 2055, and 5.0 °F to 8.0 °F (9.0 °C to 14.4 °C) for 2085. Notably, recent increases in temperature follow predicted trend



aURHNj□—Gunnison sage-grouse critical range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) as well as active, inactive, and historic Gunnison sage-grouse leks.

lines from the Global Circulation Models. Precipitation in general is more difficult to forecast (and therefore has higher uncertainty), but for the Western Great Plains is predicted to change by about 0 to –6 percent in the west and increase by 3 to 9 percent in the east by 2070 (Kunkel et al. 2013a).

In the Cold Desert, including the Wyoming Basins and Colorado Plateau, annual temperature has generally increased over the past 115 years, and in the southern portion of the ecoregion the recent 10-year averages surpass any previous decadal value. Nighttime temperatures show the greatest increase and the recent period of elevated temperatures is most prominent in spring and summer. Precipitation is highly variable and shows no long-term trend. As in the Western Great Plains, the freeze-free season length has increased especially in the south. Ensemble Global Circulation Models project a change in precipitation of 0 to –9 percent by 2070 depending on location with winter months receiving relatively more precipitation and remaining seasons less than current (Kunkel et al. 2013b).

Within both ecoregions, evapotranspiration is predicted to increase whether or not precipitation increases and even those projections that indicate increases in precipitation show decreases in water availability (Seager et al. 2007). More precipitation is falling as rain instead of snow, snowmelt is occurring earlier, and consequently there is a shift towards earlier runoff (Knowles et al. 2006). Floods and droughts are likely to become more common and more intense as regional and seasonal precipitation patterns change and rainfall becomes more concentrated into heavy events with longer, hotter dry periods in between events.

The changes in precipitation and temperature regimes described above are predicted to have large consequences for species distributions, and because individual species differ in their climatic requirements, for community composition. Warmer temperatures are leading to species distribution shifts poleward and upward in elevation—a trend that has been observed for thousands of species globally (e.g., Chen et al. 2011; Parmesan and Yohe 2003; Root et al. 2003).

Bioclimate envelope models for big sagebrush (*A. tridentata* spp.) and other sagebrush species project large decreases in southern latitudes and lower elevations, but relatively small increases in northern latitudes and higher elevations (Bradley 2010; Homer et al. 2015; Schlaepfer et al. 2012; Still and Richardson 2015). For Wyoming big sagebrush, which occupies the warmest and driest portions of the species' range, a 39 percent reduction (66 million hectares) in suitable climate is predicted by mid-century (Still and Richardson 2015). Areas in these regions that retain or gain climate suitability include higher elevations in the Cold Desert and the Northern Great Plains overall. For juniper and piñon woodlands, habitat with suitable climate is projected to move north and upslope with principal gains in Colorado and southwest Wyoming and losses in the Southwest (Rehfeldt et al. 2006, 2012).

Climate change is also predicted to have significant effects on invasive annual grasses. Cheatgrass will likely spread upwards in elevation and possibly shift to northeast facing slopes; red brome (*B. rubens*) might expand northward and/or increase its abundance in the Cold Desert and Colorado Plateau (Bradley et al. 2016). Decreases in average summer precipitation or prolonged summer droughts could enable cheatgrass invasion into sagebrush ecosystems that are currently resistant to invasion and resilient to fire disturbance (Mealor et al. 2012; Bradley et al. 2016). If average summer, plant available water declines, the land area susceptible to cheatgrass invasion may increase by up to 45 percent, particularly in mountain big sagebrush steppe in Montana and higher elevation areas of the Colorado Plateau (Bradley et al. 2016).

Greater climate variability likely will favor invasion of annual invasive species in many areas (Bradley 2010) and negatively affect native species' persistence in areas that remain otherwise climatically suitable. Reduced soil moisture availability coupled with greater climate variability can result in reduced resilience and/or recovery potential of native ecosystems following disturbances such as improper livestock grazing and uncharacteristic wildfire (Chambers et al. 2014a,b). In turn, decreased resilience can lower resistance of these ecosystems to invasive annual grasses like cheatgrass, red brome, and field brome (Chambers et al. 2014b).

Climate-driven changes are likely to combine with both persistent ecosystem and land use and development induced stresses to further increase the vulnerability of natural ecosystems to pests, disease, invasive species, and loss of native species. Changes in temperature and precipitation affect the composition and diversity of native animals and plants by altering their breeding patterns, water and food supply,

and habitat availability. In a changing climate, populations of some pests, such as mosquitos that are better adapted to a warmer climate, are projected to increase resulting in an increase in diseases such as West Nile virus, which is a threat to GRSG and GUSG (Schrag et al. 2010; USFWS 2014a).

tZVxnPjZVxjqj"45CjV6zSNjZ6P

The effects of land use and development on ecosystem resilience are diverse, but here we focus on changes in native species composition, degradation of soils, increases in exotic annual grasses and other invasive plants, and altered fire regimes. We include land fragmentation because of its importance to ecosystem processes such as species movements and gene flow. More detailed reviews of land use and development effects on sage-grouse are in Hanser et al. (2011) and Knick et al. (2011).

Livestock Grazing

Livestock grazing is the most widespread land use in the eastern portion of GRSG range. Grazing has well-recognized effects on ecosystem composition, pattern, and function (Beck and Mitchell 2000; Boyd et al. 2014a; Cagney et al. 2010; Freilich et al. 2003; Fuhlendorf and Engle 2001; Knick et al. 2011). In the COT Report (USFWS 2013), improper livestock grazing was considered a persistent and widespread threat to GRSG in Management Zones II and VII, except for three GRSG populations in Management Zone II (Jackson Hole, Wyoming, Rich-Morgan-Summit and Uintah, Utah) where it was not considered a threat. Livestock grazing occurs throughout Management Zone VII in the GUSG range and is considered a current and future threat to grouse where grazing occurs in a manner incompatible with local ecological conditions (USFWS 2014a).

The potential landscape effects of livestock grazing have been difficult to evaluate until recently because of a lack of area-wide spatial data (Knick et al. 2011). To address this lack of data, Veblen et al. (2011) compiled spatial allotment boundaries for all BLM grazing allotments and combined those spatial boundaries with tabular data from the Rangeland Administration System, including billed animal unit months (AUMs), type of animal, and season of use by pasture and allotment. Veblen et al. (2011) demonstrated that allotment spatial data can be combined with other allotment-related data, for example BLM's land health data, and with additional spatial vegetation data to examine relationships between livestock grazing and vegetation. Veblen et al. (2011) suggested that these types of analyses could assist managers in identifying allotments where livestock were potentially the cause of not meeting land health standards and prioritizing allotments for further evaluation. Similar data are being used to model vegetation phenology, timing of grazing, and intensity of grazing by allotment to relate spatial data for male GRSG reproductive success to the multivariate effects of livestock grazing on management units (Adrian Monroe, Colorado State University, personal communication).

Currently, the BLM maintains grazing allotment boundary data in a geospatial format at BLM State offices. The data are compiled at the national level and include allotment numbers by State that are related to the information tracked in the Rangeland Administration System. Livestock effects on sagebrush ecosystems and GRSG habitat at mid to local scales are evaluated on a case-by-case basis that typically does not involve spatial data analyses.

Major differences in plant responses to herbivory exist among ecoregions due to evolutionary adaptations to grazing and browsing, plant phenology relative to the timing of grazing, and selectivity of grazers for different plant species within the community. Plants in the Cold Deserts evolved without large numbers of grazing animals (Mack and Thompson 1982). In contrast, plants in the West-Central Semiarid Prairies were grazed regularly and have adapted to regular defoliation (Coughenour 1985). In the Western Cordillera colder and snow-covered winter landscapes protected low-statured plants from grazing until the growing season when moisture was available and plants typically evolved without large numbers of grazers.

Season of defoliation relative to availability of water for plant regrowth after defoliation is an important factor related to livestock grazing and plant tolerance of defoliation. Water storage and plant growth in the Cold Deserts depend on winter precipitation, especially in the western portion of the range (fig. 4). Cool-season plants (C_3 photosynthesis pathway) dominate plant communities in this ecoregion. Generally, water becomes limiting during late spring and perennial plants become dormant if they are not able to extract deep-soil moisture or able to photosynthesize during the heat of summer. The West-Central Semiarid Prairies have more available moisture during summer and have a mixture of cool-season plants and warm-season (C_4 photosynthesis) grasses that have greater water use efficiency.

Livestock effects on sagebrush ecosystems are likely more pronounced in Cold Deserts where stocking rates (Briske et al. 2011) and grazing season together can affect plant responses to grazing (Briske and Richards 1995). In Cold Deserts, defoliation of perennial grasses during inflorescence development (late spring) is the time when moisture is becoming limited and plant regrowth and recovery may be compromised (Briske and Richards 1995). In the Western Cordillera and West-Central Semiarid Prairies, precipitation during the growing season may allow greater tolerance to grazing, but cool-season grasses can be eliminated by seasonal use that impacts them yet allows warm-season plants to remain ungrazed. Care must be exercised regarding grazing season of use and stocking rates to maintain combinations of phenologically diverse plants where they should occur in these ecosystems.

The greatest potential for livestock grazing to affect sage-grouse habitat is by changing composition, structure, and productivity of herbaceous plants used for nesting/early brood-rearing (Beck and Mitchell 2000; Boyd et al. 2014a; Cagney et al. 2010; Hockett 2002). Empirical studies and meta-analysis indicate that sage-grouse nesting and early brood micro-habitat selection and brood-rearing success are closely tied to areas with greater sagebrush and grass canopy cover and height than are randomly available in sagebrush landscapes (Dinkins et al. 2016; Doherty et al. 2011a; 2014; Hagen et al. 2007; Kirol et al. 2012; Thompson et al. 2006). Grass height in particular has been shown to influence nest success for GRSG in Management Zone I (Doherty et al. 2011a; 2014). However, Holloran et al. (2005) and Dinkins et al. (2016) reported weak, if any, effects of grass height on GRSG nest success in Management Zone II. Most recently, Gibson et al. (2016) demonstrated sampling bias based on the timing of grass height data collection. Their results suggest previously published grass height results based on data collected when nest fate was determined rather than the predicted hatch date were biased

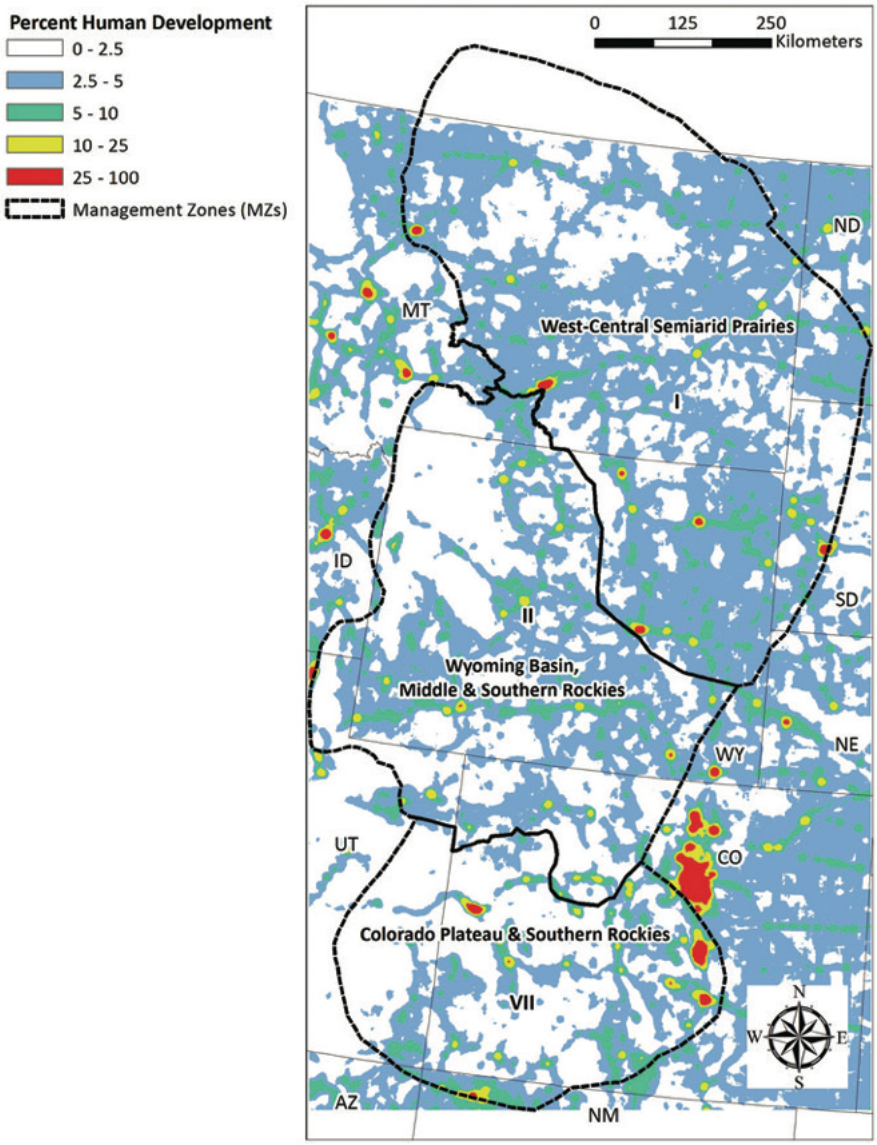
towards higher grass height relative to the true effect. In some cases, this bias was enough to change the overall direction of the effect as well as its magnitude. Therefore, revisiting management prescriptions based on specific grass heights within nesting habitat is advised. Nevertheless, repeated heavy grazing of sagebrush bunchgrass communities in Management Zone II removes bunchgrasses and leads to a sagebrush/rhizomatous grass or bluegrass state, which has reduced resource value for nesting and brood-rearing GRSG (Cagney et al. 2010). Sagebrush cover is inherently lower in the West-Central Semiarid Prairies than in other portions of the species range (Doherty et al. 2016; Herman-Brunson et al. 2009), suggesting greater reliance by breeding GRSG on herbaceous cover in Management Zone I than in other portions of the range.

Infrastructure related to domestic livestock grazing (e.g., water developments) can result in loss of vegetation structure and plant species diversity near these features (Rinehart and Zimmerman 2001). Also, fences to control livestock on western rangelands can contribute to collision related mortality, particularly when located on flat terrain close to leks (Stevens et al. 2012; Coates et al. 2016).

Urban and Exurban Development

Loss of sagebrush due to urban and exurban (residential) development since Anglo-American settlement is estimated at 16.0 percent for the West-Central Semiarid Prairies (Management Zone I), 18.4 percent for the Wyoming Basin and adjacent Rockies (Management Zone II), and 29.2 percent for the Colorado Plateau and adjacent Rockies (figs. 14, 15; Knick et al. 2011). In the COT Report (USFWS 2013), urban and exurban development was not considered a threat to GRSG in Management Zone I except for the Powder River Basin, Wyoming, where it was considered a localized threat. Development was considered a persistent and widespread threat in Management Zone II, particularly in outlying populations (Eagle South-Routt and Middle Park, Colorado; Laramie, Wyoming; Rich-Morgan Summit and Uintahs, Utah; and North Park, Colorado) and in Management Zone VII (Meeker-White River, Colorado). Most residential areas are on the edge of the current distribution of sagebrush and GRSG rather than within core areas, but resource use and connecting infrastructure can extend well beyond the boundaries of developed areas (fig. 16; Knick et al. 2011).

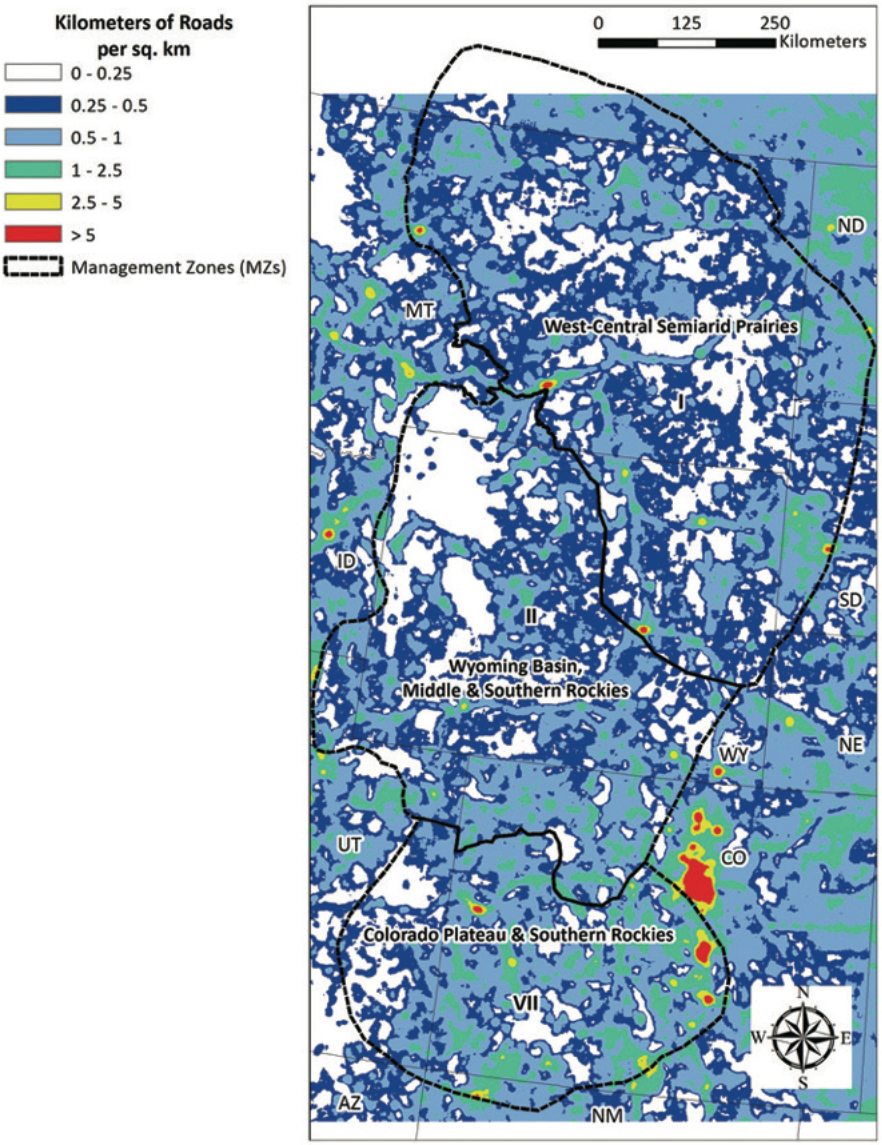
Doherty et al.'s (2016) analysis showed that human disturbance was a major factor in predicting GRSG breeding habitat in Management Zone VII (ranked #3) and a minor factor in Management Zone I (ranked #12) and Management Zone II (ranked #11). For GUSG in Management Zone VII, residential and exurban development and associated infrastructure are considered a current or potential issue in all populations (USFWS 2014a). Nesting female GUSG avoided high-density development at the landscape scale and chose to nest farther away from any single development at the patch scale (Aldridge et al. 2012). A subsequent study showed that avoidance of development resulted in no observed effects on nest survival, and it indicated that other unknown factors may be driving nest survival (Stanley et al. 2015). In general, low-density exurban developments support lower native species abundance and more human-commensal bird and mammal species and invasive plants, than comparable unfragmented rangelands (Maestas et al. 2003).



aLB(4 —Percentage of developed land (NLCD 2011) within 5.0 km of each pixel in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).



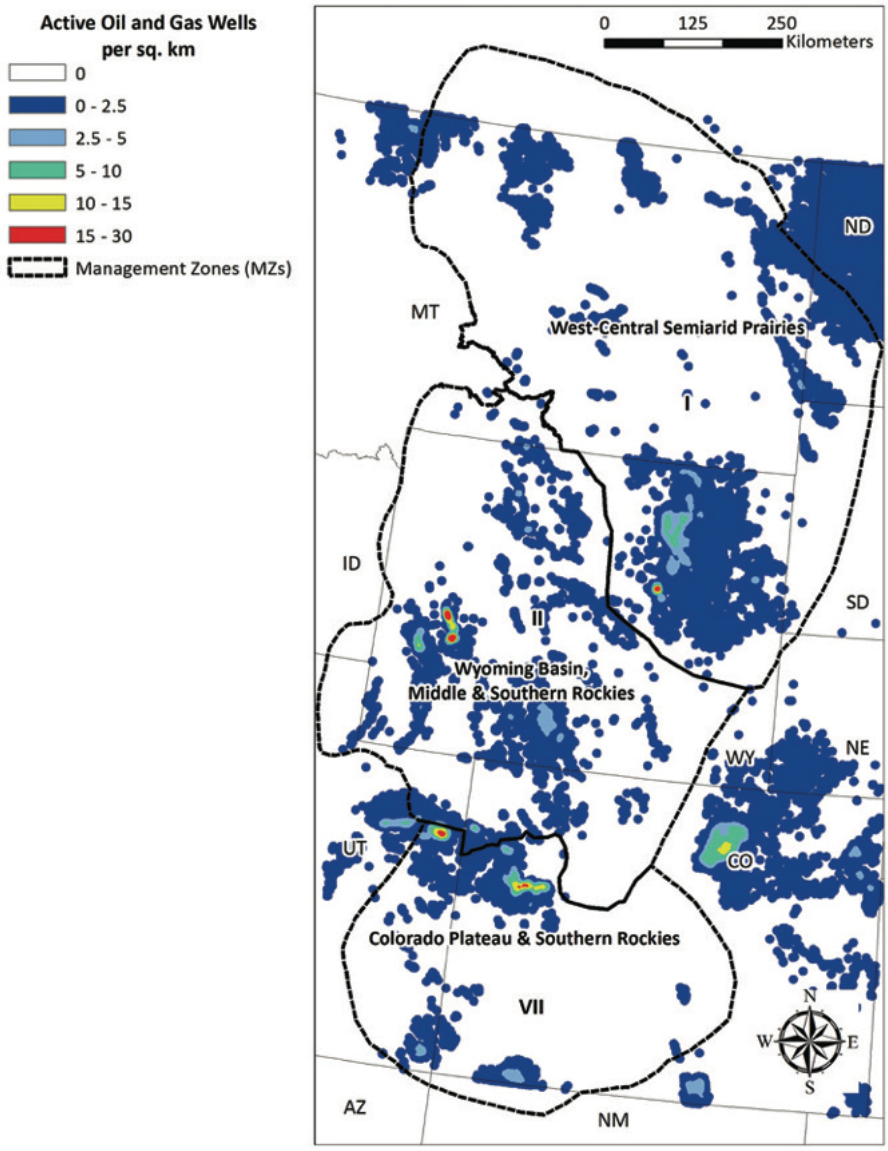
aLB(4 —Rural subdivision in Sublette County, Wyoming (photo by T. Christiansen).



aLB(4L□ —Density of all roads (surface roads, major roads, and interstate highways; ESRI Street Map Premium) in kilometers per square kilometer in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).

Energy Development

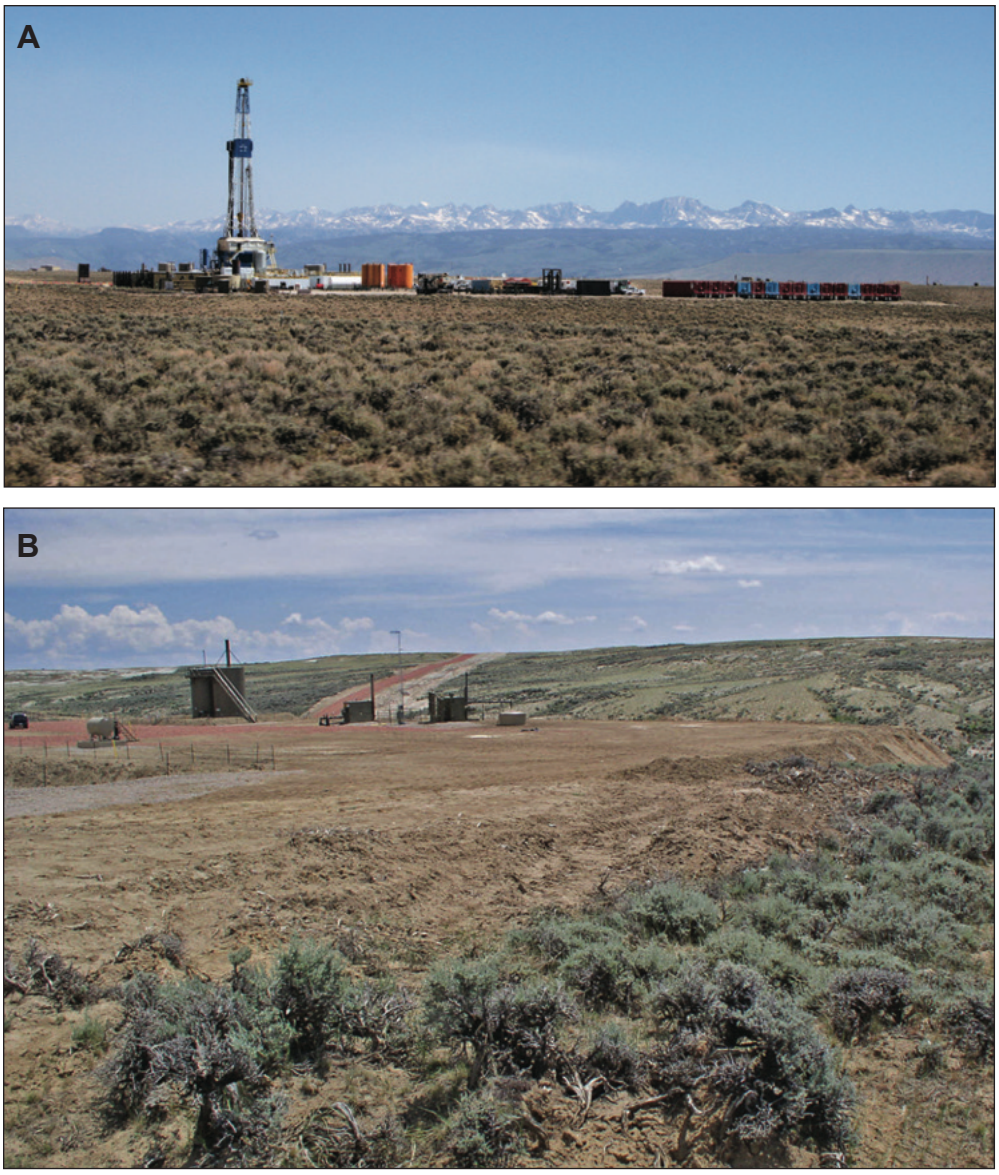
Loss of sagebrush cover associated with energy, primarily oil and gas development, has been well-documented in recent analyses. The Wyoming Basin Ecoregional Assessment (Hanser et al. 2011)—which included south-central Montana, western and central Wyoming, northeastern Utah, and northern Colorado—indicated that oil and gas development has removed approximately 658 mi^2 (1,703 km^2) of sagebrush and other native habitats in this area since 1900. This is due to construction of well pads and supporting infrastructure, such as roads, power lines, and pipelines (Finn and Knick 2011). It is considered a persistent and widespread threat to almost all GRSG populations in the eastern range (figs. 17, 18; USFWS 2013). In the COT Report (USFWS



aURHNj□—Number of active oil and gas wells per square kilometer (IHS; BLM [AFMSS]) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).

2013), energy development was considered a persistent and widespread threat to GRSG in Management Zones I, II, and VII except in two GRSG populations in Management Zone II, where it is a localized threat (Jackson Hole, Wyoming, and Uintah, Utah). Energy development is limited in the GUSG range of Management Zone VII. Only two populations, San Miguel, Colorado, and Dove Creek/Monticello, Utah, currently have a moderate level of oil and gas development and a high level of future development potential. A medium level of potential development occurs in the Crawford, Colorado, population and no other populations have potential for energy development (GSGRSC 2005; USFWS 2014a).

Removal of sagebrush vegetation as a function of energy development can increase soil resources, such as available nitrogen, and alter soil properties that can favor various invasive species (Bergquist et al. 2007; Nielson et al. 2011). When compared to sites not influenced by development activities, sites disturbed by



aURHNj□ —Deep gas drill rig (A) outside of Pinedale, Wyoming (photo by T. Christiansen), and well pad (B) (photo by K. Henke).

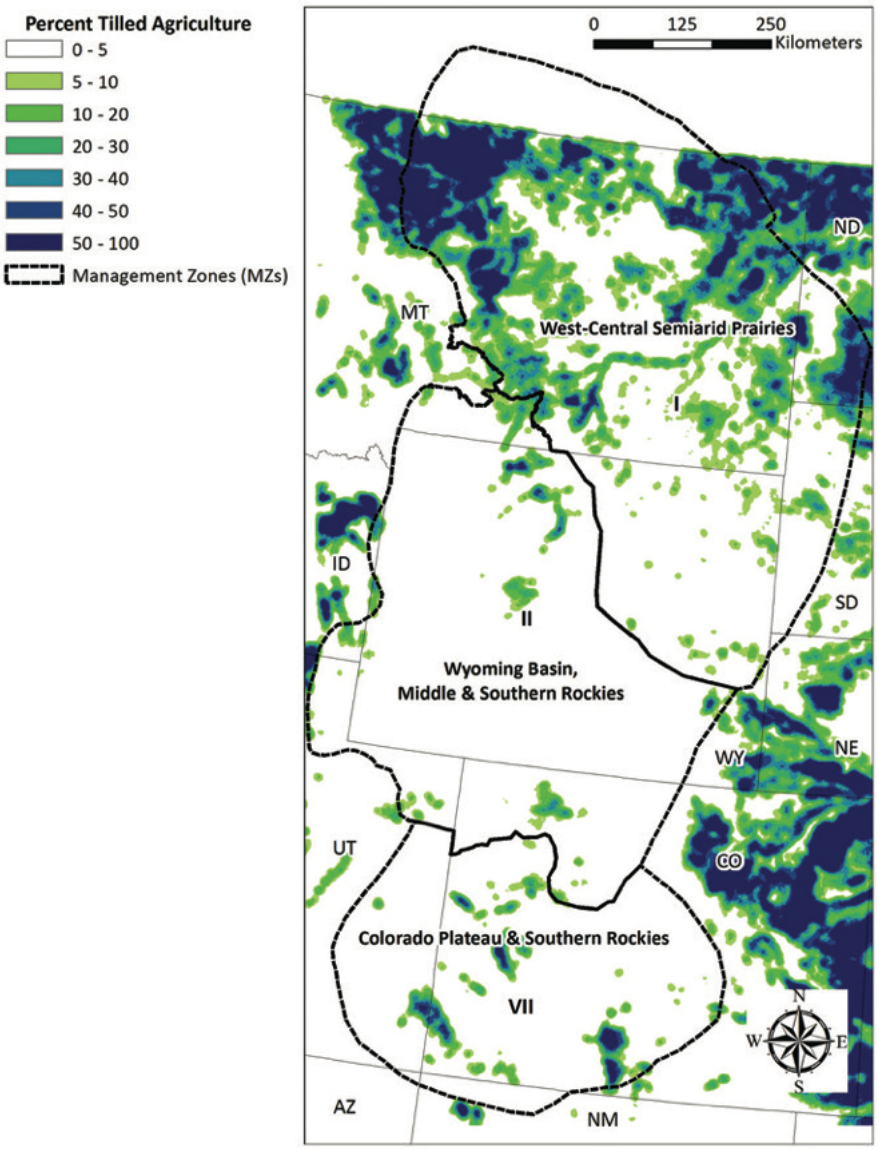
energy development had higher species richness (numbers) of exotic than native species and cover of exotic species was similar to that of native species (Bergquist et al. 2007). Similar effects have been documented for croplands and populated areas (Nielson et al. 2011). Invasive plant species are also associated with development infrastructure such as roads, highways, oil and gas well pads, pipelines, and power lines (Manier et al. 2011; 2014; Nielson et al. 2011). Although many invasive species decline at distances beyond 164 to 328 ft (50 to 100 m) of these structures, several species, including halogeton (*Halogeton glomeratus*) and cheatgrass, show low rates of decline in abundance with increasing distance from roads and reclaimed sites (Manier et al. 2011). Once these species are established, restoration is much more difficult, especially in areas with warm or dry soil temperature and moisture regimes (Pyke 2011).

Effects of development on effectiveness of sagebrush communities for GRSG and GUSG interact with other disturbance processes such as wildfire and drought. In southwest Wyoming, 10 to 15 percent of sagebrush ecosystem changes in the area were directly related to land use and development disturbances (Xian et al. 2011). Decreases in precipitation and increases in temperature between 1996 and 2006 appeared to impact sagebrush communities across all canopy cover ranges by increasing the extent of bare ground and reducing herbaceous cover (Xian et al. 2011). Also, fires that occurred largely after 1996 accounted for approximately 12 to 23 percent of the changes in sagebrush landscape cover (Xian et al. 2011). This suggests that land use and development can decrease ecosystem resilience by reducing resistance to invasive species, which in turn may increase fire frequency and extent. These effects may be most evident for sites with relatively warm or dry soil temperature and moisture regimes, and may increase as the climate warms.

A number of studies indicate that energy development activities have significant effects on GRSG and can result in localized extirpations of GRSG populations (Aldridge and Boyce 2007; Duncan 2010; Gregory and Beck 2014; Harju et al. 2010; Walker et al. 2007). Infrastructure related to energy development (e.g., roads, pipelines, storage facilities, mines, wind turbines, transmission lines) decreases the effectiveness of habitat for GRSG (Braun et al. 2002; Dinkins et al. 2014a,b; Doherty et al. 2008; Kirol et al. 2015a; LeBeau et al. 2014; Lyon and Anderson 2003). Greater sage-grouse hens with successful nests located their nests farther from roads in oil and gas fields than unsuccessful hens (Lyon and Anderson 2003). Transmission towers potentially provide perches and nesting structures for raptors and ravens, and may also contribute to collision mortalities (Beck et al. 2006; Borell 1939; Coates et al. 2014; Howe et al. 2014). Proximity to distribution and transmission lines was related to lower adult female survival for GRSG, which was most likely related to increased raptor densities rather than collision mortalities (Dinkins et al. 2014b). Also, West Nile virus and increased abundance of mesocarnivores, both of which are associated with reservoirs created to hold water produced from energy development, can cause declines in GRSG populations (Taylor et al. 2013). Thus, measures to decrease fragmentation and maintain areas with greater sagebrush cover in higher ecological condition are primary management objectives (Aldridge and Boyce 2007; Kirol et al. 2015b).

Cropland Conversion

Cropland conversion (changing rangeland to cropland) was ranked a persistent and widespread threat in areas with higher precipitation and more productive soils across the eastern range in the COT Report (USFWS 2013; Yellowstone Watershed, Montana; Eagle South-Routt and Middle Park, Colorado; North Park and Northwest Colorado [Wyoming Basin in Colorado]; Meeker-White River, Colorado) (figs. 19, 20). It was not a threat for most other populations. In Doherty et al.'s (2016) analysis, amount of tilled cropland was a minor factor in predicting GRSG breeding habitat in Management Zone I (ranked #7) and Management Zone II (ranked #14). Effects of cropland conversion may be underestimated as many productive lands with deeper soils that supported GRSG habitat historically were among the first lands converted to cropland (Vander Haegen et al. 2000). These lands are no longer considered in analyses of GRSG within their current range. Throughout GUSG range in Management Zone VII, the amount of land in cropland is declining except in the Dove Creek/Monticello, Utah, population (GSGRSC 2005) and is not expected to be a future threat in any of the other populations (USFWS 2104a).



aLB(4 —Percent annually tilled agricultural land (cropland; NASS 2014) within 5.0 km of each pixel in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016).



—Conversion of a sagebrush ecosystem in the West-Central Semiarid Prairies to agricultural land (photo by J. Carlson, used with permission).

Extensive cultivation and fragmentation of native habitats have been associated with sage-grouse population declines. The West-Central Semiarid Prairies (Management Zone I) have the highest percentage of private lands and highest amount of tilled cropland (Doherty et al. 2016). Sage-grouse are known to use agricultural fields periodically, such as for strutting grounds and brood-rearing habitat, but pesticide contamination is a documented concern (Blus et al. 1989; Connelly et al. 2000). The amount and configuration of sagebrush habitat in the landscape surrounding agricultural fields influence habitat use (Schroeder and Vander Haegen 2011). Several studies indicate that GRSG populations cannot persist in areas with less than 25 percent landscape cover of sagebrush (Aldridge et al. 2008; Knick et al. 2013; Wisdom et al. 2011). Greater sage-grouse extirpations have occurred in areas where cultivated crops exceeded 25 percent (Aldridge et al. 2008), and recent studies show that 96 percent of active leks are surrounded by less than 15 percent cropland in Management Zone I (SGI 2015; Smith et al. 2016). Management aimed at maintaining existing functional patches of sagebrush habitat at landscape scales is fundamental to the persistence of GRSG in Management Zone I.

Recreation

Recreational activities (off-highway vehicle [OHV] use, mountain biking, camping, snowmobiling, etc.) can have both direct and indirect impacts on sagebrush ecosystems and sage-grouse (USDI BLM 2009). Recreational use of OHVs is one of the fastest growing outdoor activities, although the effects of OHV use on sagebrush and sage-grouse have not been studied (Knick et al. 2011). Motorized access for recreation has a variety of effects, including removal of sagebrush cover, modification of animal behavior because of habitat changes or noise, alteration of the physical and chemical environment, and spread of invasive plants (Knick et al. 2011). In the COT Report (USFWS 2013) recreation is considered a persistent and widespread threat or a localized threat in every population in Management Zone I and Management Zone II, except the Meeker-White River and Parachute-Piceance-Roan populations in Colorado. Recreational use within the GUSG range is widespread, occurs throughout the year, and has expanded as more people move into the area or travel to recreate (Connelly et al. 2004). Recreation uses have affected large areas of GUSG range, especially portions of the Gunnison Basin and Piñon Mesa populations (USFWS 2014a).

Habitat Fragmentation

Land use and development can affect both habitat loss and habitat fragmentation. In its 2010 listing decision, the U.S. Fish and Wildlife Service determined that the greatest threat to GRSG was habitat loss and fragmentation (USFWS 2010). The USFWS noted in its 2015 decision (USFWS 2015) that the configuration of sagebrush mosaics across the range of GRSG has changed, resulting in risk of increased population isolation, exposure to predators in areas of edge habitat, and invasive plants (Gelbard and Belnap 2003; Knick and Connelly 2011; Saunders et al. 1991).

Habitat fragmentation is a function of habitat configuration (e.g., number of habitat fragments, edge density, patch shape), rather than total amount of habitat in a landscape. “Fragmentation” represents the dissection of large expanses of habitat via various mechanisms (Manier et al. 2013). Greater sage-grouse populations

generally rely on large, interconnected expanses of sagebrush for local migrations and access to seasonal habitats (Connelly et al. 2004, 2011a,b). While conclusive data establishing minimum sizes of sagebrush-dominated landscapes necessary to support populations of GRSG are unavailable (Connelly et al. 2011a,b), some quantitative indications exist. For example, research in Wyoming and Montana suggest that the size of a sagebrush dominated landscape needed to support breeding habitats of an interspersed population may exceed 386 mi^2 (1,000 km^2) (Doherty et al. 2008). Investigations from Idaho and Wyoming suggest that relatively large blocks of sagebrush habitat (>9,884 acres [4,000 ha]) are critical to successful reproduction and overwinter survival (Leonard et al. 2000; Walker et al. 2007; Wisdom et al. 2011). More recently, Doherty et al. (2016) developed a spatial model of occupied GRSG breeding habitat based on biophysical habitat, climate, landform, and anthropogenic development. This model clearly shows the importance of ecological context in determining both habitat selection and response to disturbance.

Reduction and fragmentation of sagebrush habitats can decrease GRSG abundance and reduce the distribution of GRSG across the landscape (Knick et al. 2011; Leu and Hanser 2011). Greater sage-grouse avoid habitats near anthropogenic infrastructure associated with energy development (Naugle et al. 2011), interstate highways (Connelly et al. 2004; Knick et al. 2013), cropland (Aldridge and Boyce 2007; Smith et al. 2005; Walker et al. 2007,) and urban and exurban subdivision development (Aldridge and Boyce 2007). Indirect effects such as increased mortality and reduced reproductive success have also been documented.

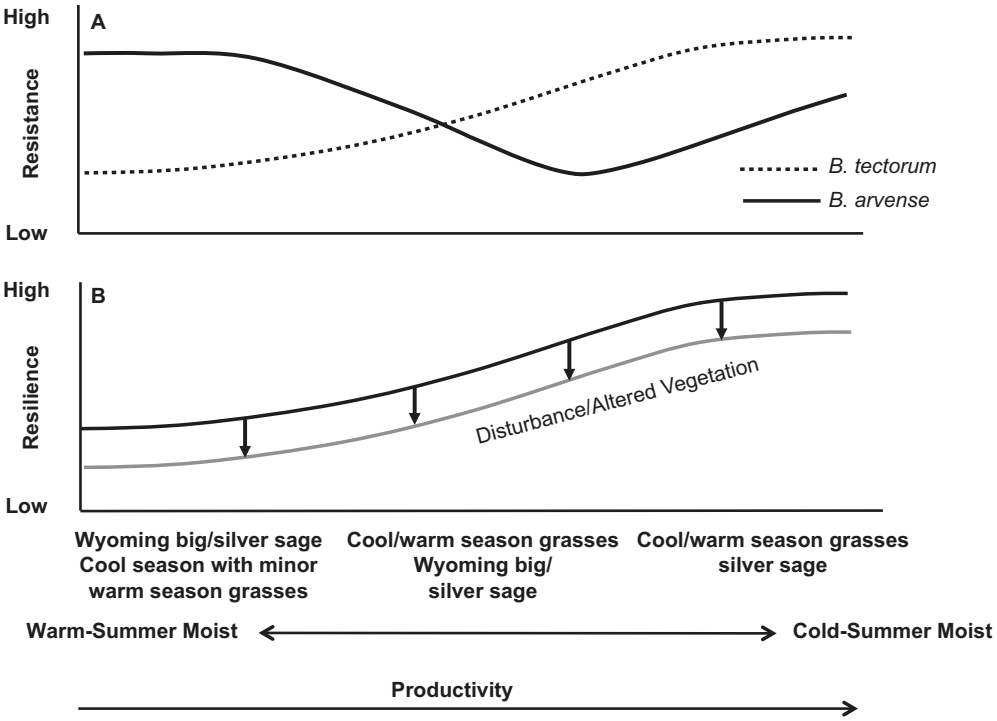
The historic distribution of GUSG was naturally fragmented by piñon-juniper and rocky canyons (Braun et al. 2014; Rogers 1964). In 2014, the GUSG was listed as threatened by the U.S. Fish and Wildlife Service. In the determination document for the listing, habitat loss, degradation, and anthropogenic fragmentation of sagebrush habitats were considered the primary causes of GUSG decline in abundance and distribution (USFWS 2014a). Between 1958 and 1993 substantial sagebrush was lost; Gunnison Basin showed an 11 percent loss in sagebrush acreage, with a 28 percent loss combined for satellite populations (Oyler-McCance et al. 2001). This resulted in considerable habitat fragmentation with remnant sagebrush patches surrounded by a matrix of unsuitable habitat for GUSG. Due to habitat loss and fragmentation, the seven populations have become isolated with limited migration and gene flow thus increasing the likelihood of extirpation (USFWS 2014a).

Current climate and climate change are important factors determining the negative effects of habitat loss and fragmentation on species density and/or diversity (Mantyka-Pringle 2011). Most studies indicate that current habitat loss and fragmentation outweigh the responses of climate warming on species and ecosystems (Franco et al. 2006; Jetz et al. 2007), but the impact of climate change is predicted to increase over time and may exacerbate land-use modifications in determining population trends (Lemoine et al. 2007). Populations in fragmented landscapes are more vulnerable to environmental drivers, such as climate change, than those in continuous, intact landscapes (Opdam and Wascher 2004; Travis 2003). Also, the threshold of climate change below which species extinction occurs or populations severely decline is likely to be determined by the pattern of habitat loss (Opdam and Wascher 2004).

Nonnative Invasive Plant Species

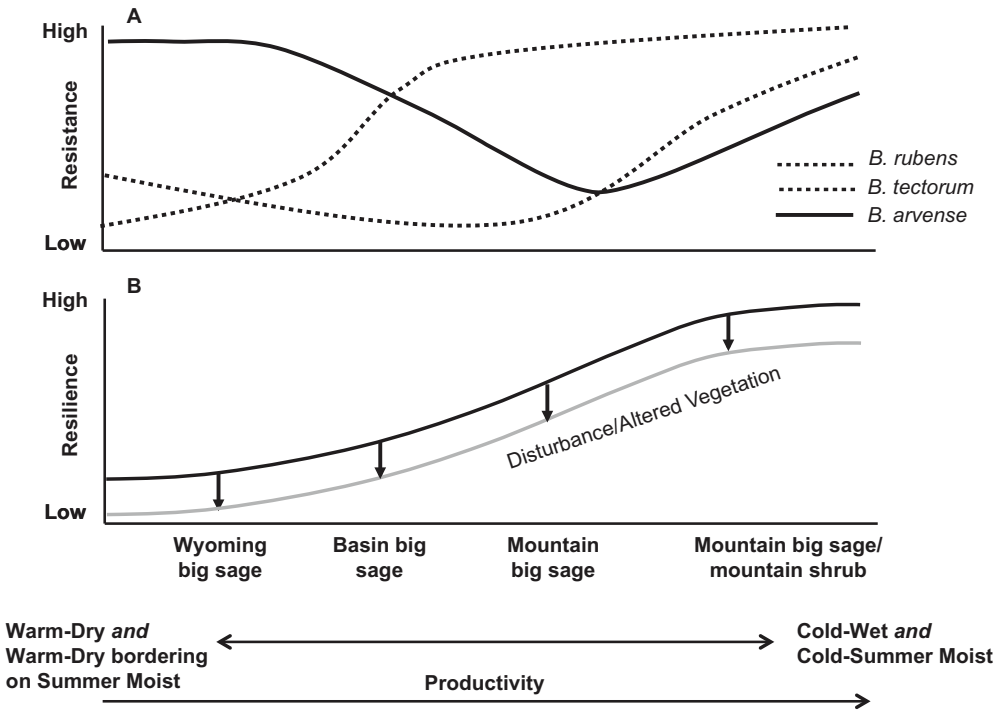
Our ability to address persistent ecosystem and land use and development threats to sagebrush habitats can be greatly enhanced by understanding the effects of environmental conditions on resilience to stress and disturbance and resistance to invasion by nonnative plants (Chambers et al. 2014a,b; Wisdom and Chambers 2009). In the West-Central Semiarid Prairies, Western Cordillera, and Cold Deserts, resilience of native ecosystems to stress and disturbance changes along climatic and topographic gradients at both landscape and local scales. At landscape scales, higher precipitation and cooler temperatures, along with greater soil development and plant productivity, typically result in greater resource availability and more favorable environmental conditions for plant growth and reproduction (Alexander et al. 1993; Dahlgren et al. 1997). In contrast, lower precipitation and higher temperatures result in reduced resource availability for plant growth and reproduction and thus lower ecosystem productivity (Smith and Nowak 1990; West 1983a,b). Higher levels of available resources coupled with greater productivity generally result in increased ecosystem resilience to disturbances and management treatments (Chambers et al. 2014a,b). More resilient ecosystems typically exhibit smaller changes following perturbations and recover more rapidly than less resilient ecosystems (Chambers et al. 2014a,b; Davies et al. 2012). These relationships also are observed at local or site scales where aspect, slope, and topographic position affect solar radiation, erosion processes, and effective precipitation, and thus soil development and vegetation composition and structure (Condon et al. 2011; Johnson and Miller 2006).

Resistance to nonnative invasive plant species depends on environmental factors and ecosystem attributes and is a function of (1) the invasive species' physiological and life history requirements for establishment, growth, and reproduction; and (2) interactions with the native perennial plant community including interspecific competition and response to herbivory and pathogens. Soil temperature and moisture regimes strongly influence plant species distributions and relative abundances. The importance of these factors in determining invasibility is well-illustrated for nonnative invasive brome grasses, which are among the most widespread and problematic invasive plant species in sagebrush ecosystems (figs. 21, 22; Brooks et al. 2016; Chambers et al. 2014b; 2016a). For example, germination, growth, and/or reproduction of cheatgrass is physiologically limited in relatively warm and dry sites at lower elevations by frequent, low precipitation years, constrained by low soil temperatures at high elevations, and optimal under relatively moderate temperature and water availability at mid elevations (Chambers et al. 2007; Meyer et al. 2001). In contrast, red brome is found primarily on warm and dry salt desert sites (Salo 2005). Field brome is limited on warm and dry as well as cold sites but is relatively abundant on cool and moist sites (Baskin and Baskin 1981). Slope, aspect, and soil characteristics modify soil temperature and water availability and influence resistance to brome grasses at landscape to plant community scales (Chambers et al. 2007; Condon et al. 2011; Mealor et al. 2013; 2014; Reisner et al. 2013; 2015; Salo 2005).



aURHNj —Resistance to invasive annual brome grasses (A) and resilience to disturbance (B) over a typical soil moisture and temperature gradient in the West-Central Semiarid Prairies. Dominant ecological sites occur along a continuum from relatively warm and summer moist with Wyoming big sagebrush, silver sagebrush, and cool season grasses with a minor component of warm season grasses to cold and summer moist with a mixture of cool and warm season grasses and silver sagebrush. Resistance to annual brome grasses varies along the temperature and precipitation gradient as a function of their ecological amplitudes and is affected by disturbances and management treatments that alter vegetation structure and composition and increase resource availability. Resilience also increases along the gradient and is influenced by site characteristics like soils and aspect (based on Chambers et al. 2014b).

The occurrence and persistence of invasive annual grasses in sagebrush habitats are strongly influenced by interactions with the native perennial plant community. For example, cheatgrass is a facultative winter annual that can germinate from early fall through early spring, exhibits root elongation at low soil temperatures, and has higher nutrient uptake and growth rates than most native species (Arredondo et al. 1998; James et al. 2011; Mack and Pyke 1983). Seedlings of native, perennial plant species are generally poor competitors with cheatgrass, but adults of native, perennial grasses and forbs, especially those with similar growth forms and phenology, can be highly effective competitors with the invasive annual (Blank and Morgan 2012; Booth et al. 2003; Chambers et al. 2007). Also, biological soil crusts, which are an important component of plant communities in warmer and drier sagebrush ecosystems, can reduce germination or establishment of cheatgrass (Eckert et al. 1986; Kaltenecker et al. 1999). Disturbances or management treatments that reduce abundance of native perennial grasses and biological soil crusts and increase the distances between these perennial grasses often result in higher resource availability and increased competitive ability of cheatgrass (Chambers et al. 2007; Reisner et al. 2013; 2015; Roundy et al. 2014). Similarly, decreases in native perennial grasses



LH —Resistance to invasive annual brome grasses (A) and resilience to disturbance (B) over a typical soil temperature and moisture gradient in the Cold Desert. Dominant ecological sites occur along a continuum from relatively warm and dry to cold and wet conditions that includes salt desert shrub, Wyoming big sagebrush, basin big sagebrush, mountain big sagebrush, and mountain big sagebrush with root-sprouting shrubs. Resistance to annual brome grasses varies along the temperature and precipitation gradient as a function of their ecological amplitudes and is affected by disturbances and management treatments that alter vegetation structure and composition and increase resource availability. Resilience also increases along the temperature and precipitation gradient and is influenced by site characteristics like soils and aspect (based on Chambers et al. 2014b).

and elevated resources result in increased abundances of red brome (Salo 2005), field brome (Collins et al. 1985), and also species like spotted knapweed (*Centauria stoebe* ssp. *micranthos* syn. *C. maculosa*) (Willard et al. 1988).

The type, characteristics, and natural range of variability of stress and disturbance strongly influence both resilience and resistance. Disturbances like overgrazing of perennial plants by livestock and atypical fire regimes are outside of the historical range of variability and can reduce the resilience of sagebrush ecosystems. Reduced resilience is triggered by changes in environmental factors like temperature regimes, abiotic attributes like water and nutrient availability, and biotic attributes such as vegetation structure, composition, and productivity (Chambers et al. 2014b) and cover of biological soil crusts (Reisner et al. 2013). Resistance to an invasive species can change when alterations in abiotic and biotic attributes result in increased resource availability or altered habitat suitability that influences an invasive species' ability to establish and persist and/or compete with native species (Chambers et al. 2014b,c). Progressive reduction of resilience and resistance can result in the crossing of abiotic and/or biotic thresholds and an inability of the system to recover to the reference state (Briske et al. 2008).

for Management and Inform Management Strategies

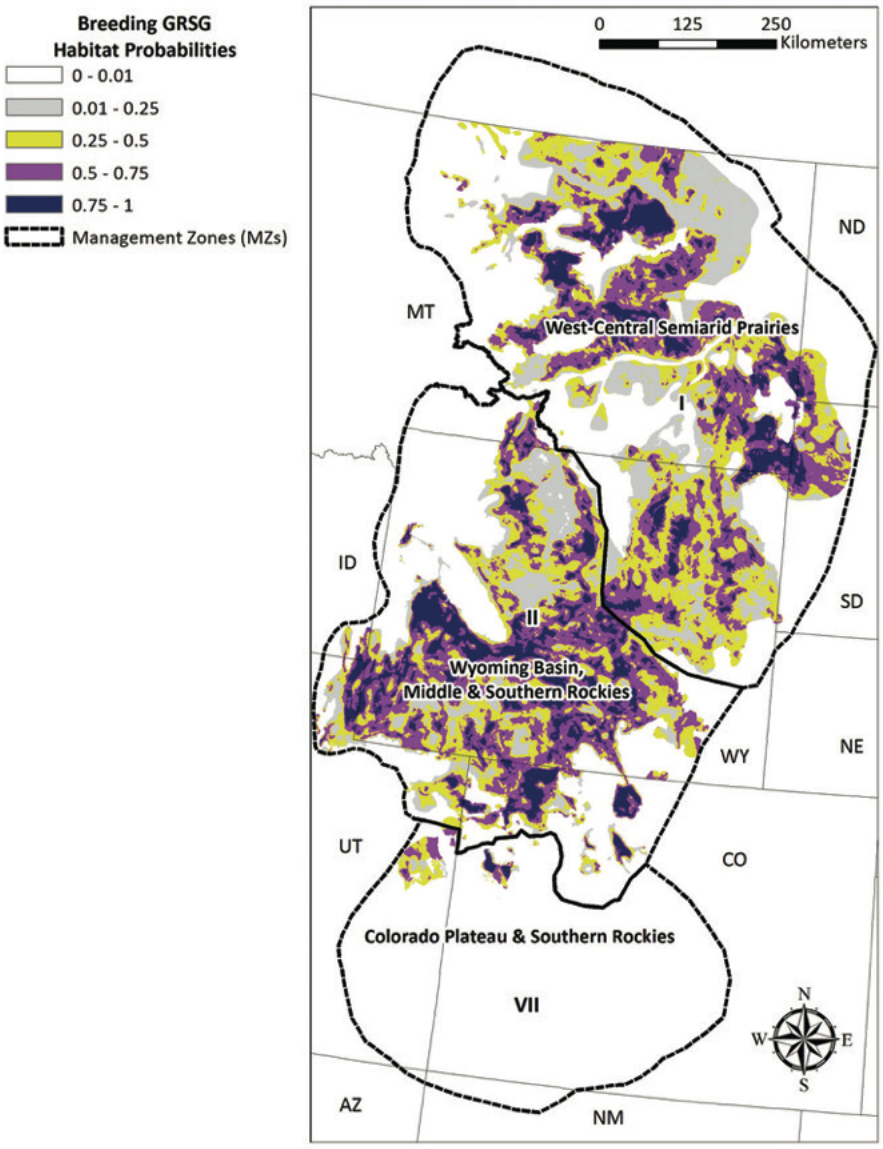
Widespread persistent ecosystem and land use and development threats coupled with large and diverse ecoregions require a strategic approach to conserve sage-grouse habitats (Meinke et al. 2009; Pyke 2011; Wisdom and Chambers 2009; Wisdom et al. 2005). This strategic approach requires the ability to (1) identify those locations that provide current or potential habitat for sage-grouse, (2) prioritize management actions based on relative resilience and resistance, and (3) effectively allocate resources to achieve desired objectives. Recently, probabilistic models of GRSG occupied breeding habitat have been developed that account for general habitat characteristics, climate, landform, and disturbance. Spatially explicit models have been developed that quantify the relative density of breeding male GRSG across Management Zones (Doherty et al. 2016). And information on the relationships of environmental characteristics to ecological types and their inherent resilience and resistance has been developed. Coupling species distribution and abundance information with relative habitat resilience and resistance provides the foundation to (1) prioritize areas for management that sustain viable populations of birds and (2) determine the most appropriate treatments based on the area's capacity to respond to management actions (Chambers et al. 2014c).

Indices

Sage-Grouse Breeding Habitat Model

We used two sets of models developed for the U.S. Fish and Wildlife Service status assessment (Doherty et al. 2016) to develop sage-grouse breeding habitat probabilities and population indices. The occupied breeding habitat distribution model (hereafter, breeding habitat model) was developed to more accurately portray important breeding areas for GRSG (Doherty et al. 2016) primarily because information available to the USFWS regarding occupied GRSG range was developed at a broad spatial scale and included large areas of unsuitable habitat. The breeding habitat model uses GRSG lek data as a proxy for landscapes important to breeding birds, because leks are central to the breeding ecology of sage-grouse (Coates et al. 2013; Holloran and Anderson 2005). The breeding habitat model evaluates characteristics such as vegetation (i.e., land cover), climate, landform, and disturbance variables around leks, which is where most nests occur (Holloran and Anderson 2005), i.e., within a radius of 4 mi (6.4 km; 13,010 ha; Doherty et al. 2016). The model provides an estimate of the probability of occupied breeding habitat at a spatial resolution of 120 x 120 m based on habitat characteristics for each sage-grouse Management Zone (fig. 23).

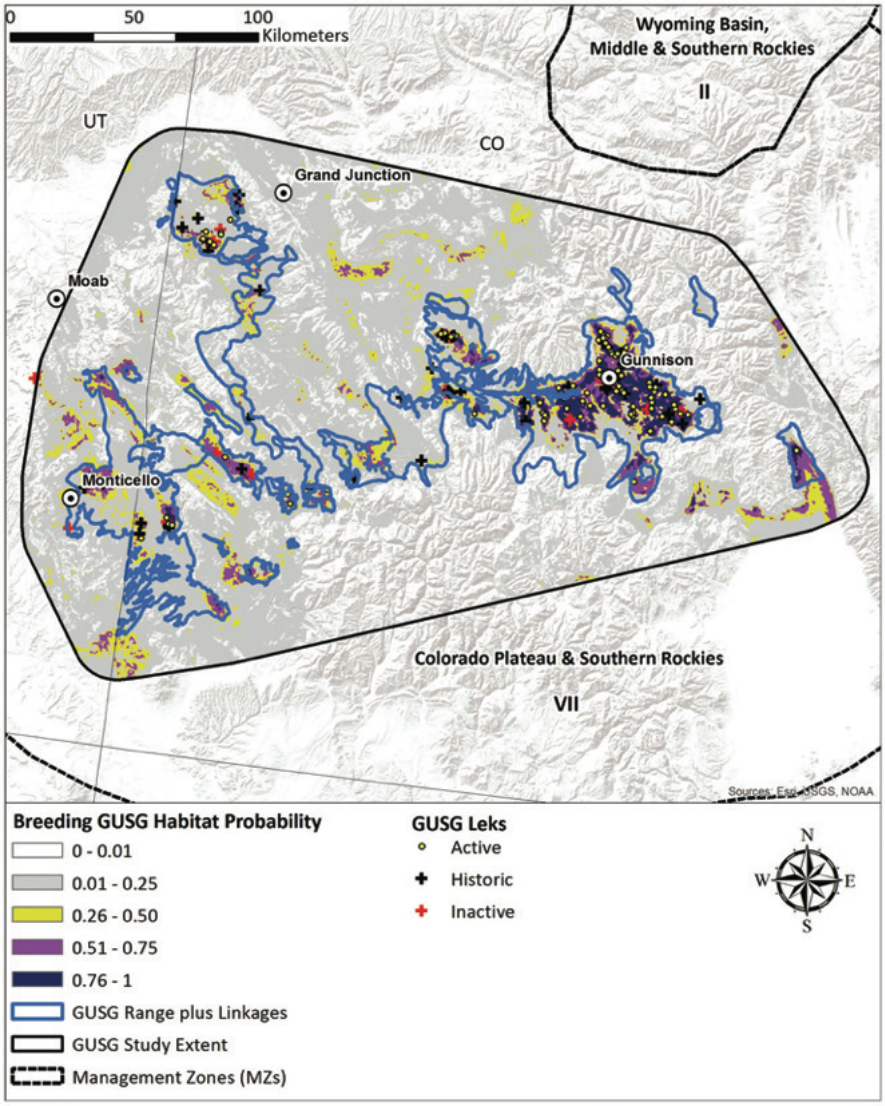
For this report, we modeled breeding habitat for GUSG in Management Zone VII following the same methodology used by Doherty et al. (2016) for GRSG. We used lek designations for active, inactive, and historic GUSG leks provided by Colorado Parks and Wildlife (GSRSC 2005) and by Utah Division of Wildlife Resources for Utah from 1995–2015. As with the GRSG breeding habitat analysis, we performed a geographic range analysis (i.e., Johnson's [1980] first order scale) to evaluate breeding habitat represented by active GUSG leks. The extent of this analysis was



aURHNj —Greater sage-grouse breeding habitat probabilities based on 2010 to 2014 lek data (Doherty et al. 2016) in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). Active leks are overlaid.

delineated by placing a minimum convex polygon around range-wide GUSG habitat defined by Colorado Parks and Wildlife as occupied range and linkage habitat, Utah Division of Wildlife Resources as occupied and unoccupied habitat, and the U.S. Fish and Wildlife Service as critical habitat. We then buffered the polygon by 11 mi (18 km) as a reasonable approximation for the average distance an individual GUSG might move during the year to access seasonal resources based on several GRSG studies from Wyoming (Fedy et al. 2012). We quantified habitat, landform, and disturbance variables within two spatial scales, 2.5 mi (4.0 km) and 0.35 mi (0.56 km) of each lek. The median distance of an active GUSG lek from non-habitat as defined by Colorado Parks and Wildlife, Utah Division of Wildlife Resources,

and the U.S. Fish and Wildlife Service (e.g., forested areas) was approximately 2.5 mi (4.0 km). We believed the smaller buffer size for GUSG compared to GRSG was warranted because a 4 mi (6.4 km) buffer placed around active GUSG leks included approximately 37 percent non-habitat (e.g., forested). We also considered a second lek buffer distance of 0.56 km (100 ha) for GUSG, which coincided with the avoidance distance of nesting GUSG from conifer in the western portion of the Gunnison Basin (Aldridge et al. 2012). Climatic variables were evaluated within 30 m x 30 m pixels. Similar to the GRSG breeding habitat model, the GUSG breeding habitat model generated an estimate of the probability of occupied breeding habitat at a spatial resolution of 30 x 30 m based on habitat characteristics within the GUSG range (fig. 24).



aURHNj□—Gunnison sage-grouse breeding habitat probabilities for the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) based on lek data from 1995 to 2015. The breeding habitat probabilities were developed for this report based on Doherty et al. 2016. Active, historic, and inactive leks are overlaid.

We used the breeding habitat probabilities for GRSG (Doherty et al. 2016) and GUSG (see above) to develop three categories of breeding habitat suitability for areas near leks that can be used to prioritize management actions on the landscape: low (0.25 to <0.50); moderate (0.50 to <0.75); and high (0.75 to 1.00). Areas with very low probabilities (0.01 to <0.25) were considered to be unsuitable for breeding habitat, but may provide habitat during other life stages or linkages between suitable breeding habitat. Greater sage-grouse leks were defined as active if more than two males were counted in a single year from 2010 to 2014 and the last count was not zero (Doherty et al. 2016). Inactive GRSG leks were defined as those where no males were observed for more than four of the last lek counts. For GUSG, we combined inactive and historic leks. We relied on the probability values at existing active lek locations for GRSG and GUSG to define thresholds in breeding habitat probabilities. We then used the probability values at inactive lek locations for GRSG and inactive and historic lek locations (combined) for GUSG to conduct an accuracy assessment of our categorization of habitat probabilities (table 2). Our goal was to categorize breeding habitat so that less than 10 percent of active leks and more than 50 percent of the inactive leks would occur in the low and moderate probability ranges. This approach clearly differentiates where management actions to improve habitat are warranted (table 2). Inactive leks in the high habitat probability range (29.7 percent for GRSG and 45.6 percent for GUSG; table 2) may reflect site-specific issues such as a small wildfire that burned habitat surrounding a lek or a road or single oil and gas well placed close to a lek that resulted in its collapse. In contrast, active GRSG leks in the unsuitable (0.1 percent of active leks) and low (0.8 percent of active leks) probability ranges would indicate leks that are at high

Table 2—Breeding habitat model probabilities for Greater sage-grouse leks in Management Zones I, II, and VII and Gunnison sage-grouse leks in Management Zone VII grouped into ranges relative to their probability of supporting sage-grouse leks. Percentage (sample size) of active and inactive Greater sage-grouse leks from Colorado, Idaho, Montana, North Dakota, South Dakota, Utah, and Wyoming are included as an illustration of the distribution of current active and inactive leks within these probability ranges. Percentage (sample size) of active and inactive Greater sage-grouse leks from all States and active and inactive/historic Gunnison sage-grouse leks from Colorado and Utah are included as justification of probability breaks for these probability ranges. Habitat probabilities for Greater sage-grouse were modeled by comparing habitat characteristics within 4 mi (6.4 km) around active leks and pseudo-absence locations (Doherty et al. 2016). Habitat probabilities for Gunnison sage-grouse were modeled by comparing habitat characteristics within 2.5 mi (4.0 km) and 0.35 mi (0.56 km) around active leks and pseudo-absence locations (this report).

	Breeding habitat probability			
Percentage of leks	TNtLBVD	r/	h/KDQLD	a1wl
Greater sage-grouse				
Active (%)	0.1 (*n* = 1)	0.8 (*n* = 14)	7.2 (*n* = 131)	92.0 (*n* = 1,680)
Inactive (%)	6.2 (*n* = 51)	24.5 (*n* = 202)	39.6 (*n* = 326)	29.7 (*n* = 244)
Gunnison sage-grouse				
Active (%)	0.0	0.0	1.1 (*n* = 1)	98.9 (*n* = 93)
Inactive/historic (%)	7.3 (*n* = 5)	22.1 (*n* = 15)	25.0 (*n* = 17)	45.6 (*n* = 31)

risk of collapse (table 2). Habitat managers should consult table 1 to identify the top predictor variables for GRSG breeding habitat in each Management Zone and for GUSG in Management Zone VII to identify specific issues. Identifying these issues may help explain why some leks occur in low, moderate, and high probability ranges. For example, there may be specific issues such as energy development structures or wildfire that eliminated sagebrush near inactive leks in the moderate probability range.

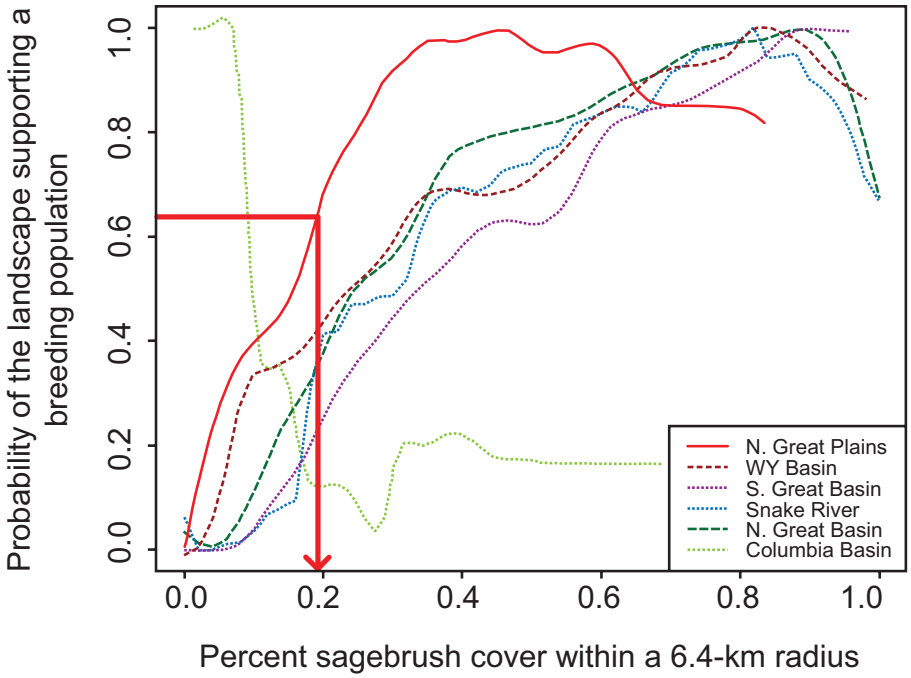
Sage-Grouse Population Index Model

Doherty et al. (2016) also developed a population index model (hereafter, population index) to identify areas on the landscape that contain population centers of male GRSG. Past work has shown that sage-grouse populations are highly clumped and that relatively small areas can contain a disproportionate number of males attending leks (Doherty et al. 2011a). This model is important because there are very large differences in the density of birds even within the identified high sage-grouse breeding habitat probability threshold described above. The population index serves as a proxy for relative abundance, which allows for better understanding of how risks, such as development or conifer expansion, and management strategies can be aligned spatially with population centers of sage-grouse. The population index model provides spatial insight into the importance of specific areas to the overall relative number of male GRSG during 2010 to 2014. Because of its threatened status under the Endangered Species Act (USFWS 2014a) and its limited distribution and abundance, we believe all GUSG range is important to the conservation of the species. However, lek locations can provide spatial insight into the relative importance of specific areas within the satellite populations of GUSG (fig. 13).

The population index model follows logic similar to previous published work by the U. S. Geological Survey on the Bi-State Greater sage-grouse population (Coates et al. 2016). To create the population index model, lek data were used to identify hotspots using kernel density functions. The kernel density function was linked with the breeding habitat model to develop a final population index model. The model created grids that represent an index to the relative abundance of breeding males in each 120 x 120 m pixel within each Management Zone. The final population index models incorporated spatial patterns of sage-grouse habitat selection with contemporary information of abundance within each Management Zone (fig. 9). Similar to the breeding habitat model, the population index model can be linked with other spatially explicit risk models or conservation actions to understand spatial overlap of habitat with sage-grouse populations. We did not develop a population index model for GUSG.

Use and Limitations of the Breeding Habitat Models

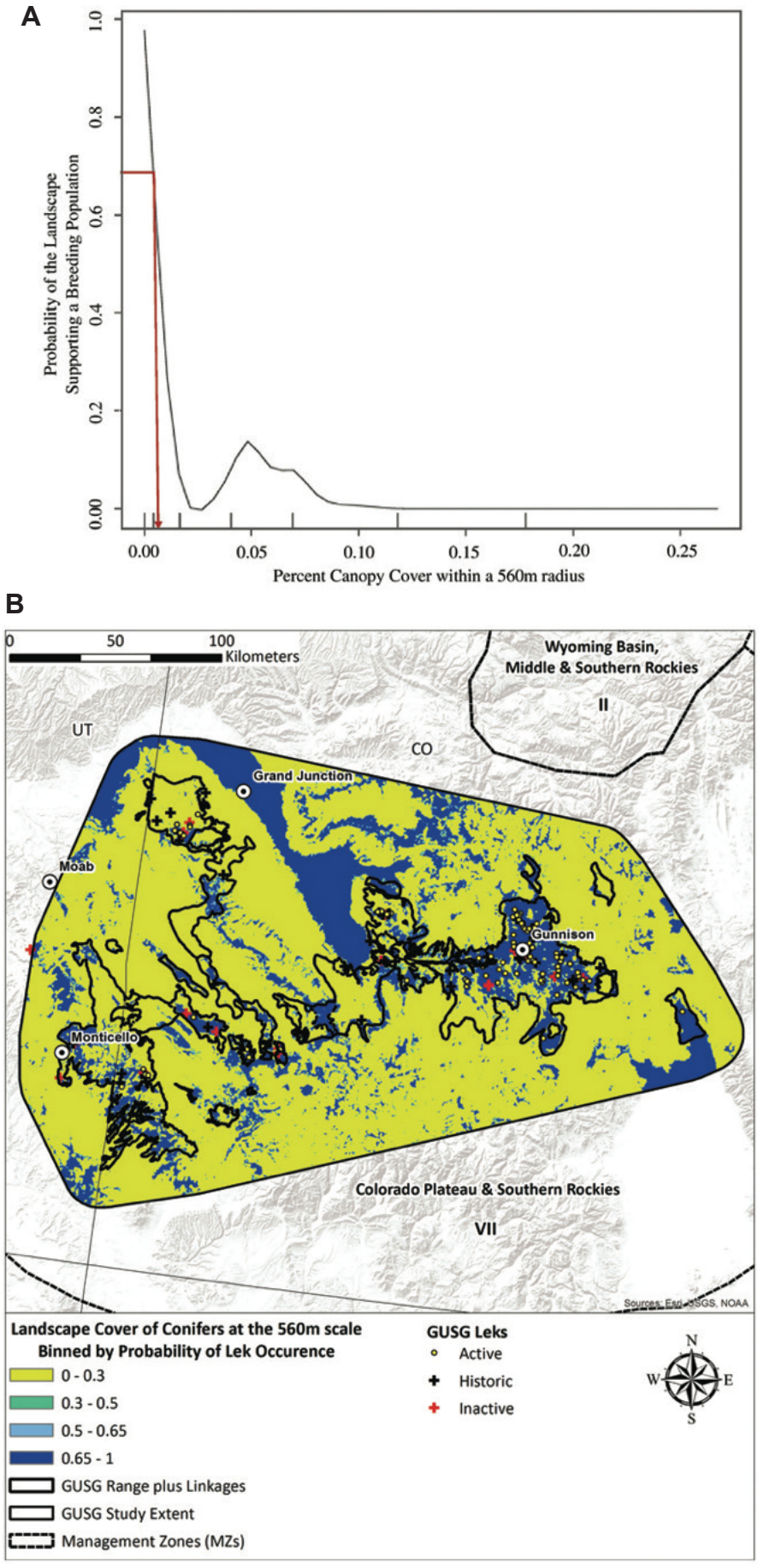
We used partial probability plots to elucidate habitat relationships of the variables in the final breeding habitat model for GRSG (Doherty et al. 2016) and GUSG. These figures demonstrate how the probability of the landscape to support a breeding population of sage-grouse changes relative to specific habitat variables (fig. 25). To improve interpretability and show variation across the GRSG range, we plotted each covariate for all Management Zones on the same plot. The partial probability plots were derived using the rfUtilities library (Evans and Murphy 2014).



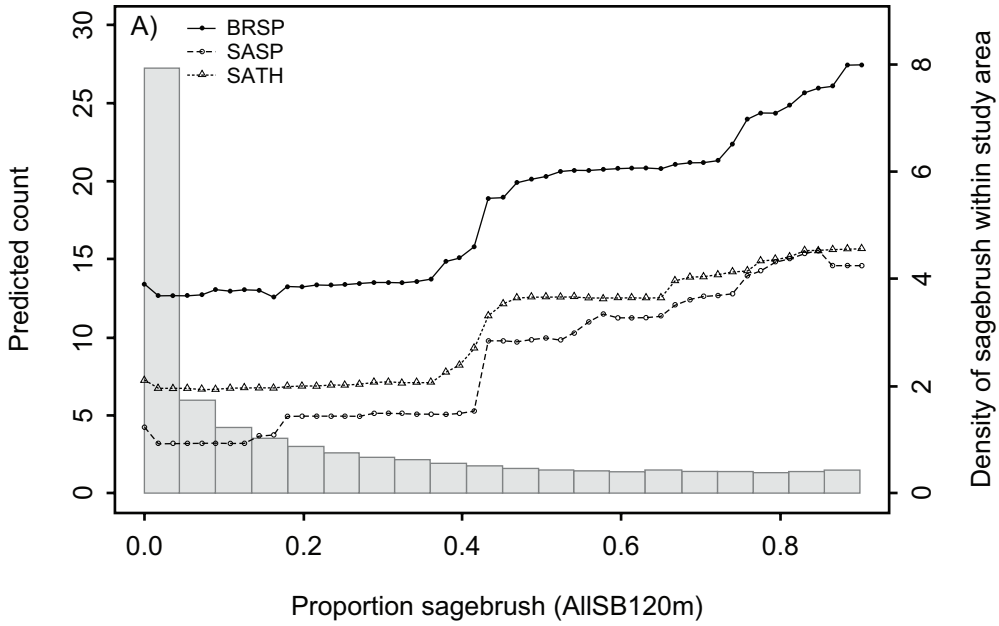
āURHNj□—Partial probability plot depicting the effect of landscape cover of sagebrush on the probability of a landscape supporting a breeding population of Greater sage-grouse (modified from Doherty et al. 2016). The thick red line shows the minimum level of sagebrush landscape cover needed to support a breeding population of Greater sage-grouse based on a 4 mi (6.4 km) radius of a lek. Landscape cover of sagebrush was derived from Landfire (USGS 2014).

Partial probability plots of habitat relationships can also be used to identify thresholds in which non-habitat features exceed the tolerance of a species. For example, within the GUSG range, steep declines in the probability of an area supporting breeding habitat were associated with greater proportion of landscape cover of conifers within 0.35 mi (0.56 km) of leks (fig. 26A). The relationship of habitat characteristics can be mapped in a Geographical Information System (GIS) to display areas that have exceeded the GUSG threshold for the probability of lek occurrence in relation to a particular habitat characteristic. To illustrate this point, we have used habitat values associated with a probability threshold of 0.65 (identified in fig. 25 for GRSG) to predict the probability of lek occurrence across the entire range of GUSG (fig. 26B). We used this threshold because the original models developed by Doherty et al. (in press) indicated that all active GRSG leks existed in areas with estimated occupied habitat probabilities greater than 0.65, and our GUSG modeling for this report indicated all active GUSG leks were in areas with estimated breeding habitat probabilities greater than 0.66.

Use of a spatially explicit model that predicts occurrence based on multiple habitat features simultaneously is preferred over using a single habitat variable such as sagebrush cover to define priority habitat areas. This is because environmental niches of species are defined by multiple variables (e.g., James 1971). However, when multi-variable, spatially explicit models do not exist, then using threshold values of a single habitat variable from the literature, such as those identified in fig. 25, can be a useful starting place for defining priority areas. For example, Donnelly et al. (in press) showed an apparent threshold value of sagebrush cover of 40 percent above which the occurrence of three sagebrush obligate passerines increased (fig. 27).



aLB(4 (A) Partial probability plot depicting the effect of landscape cover of conifers on the probability of a landscape supporting a breeding population of Gunnison sage-grouse. The red line shows the maximum level of conifer land cover that can support a breeding population of Gunnison sage-grouse based on a 0.35 mi (0.56 km) radius of a lek. (B) Spatial depiction of the landscape cover of conifers binned by the predicted probability of Gunnison sage-grouse lek occurrence using a 0.35 mi (0.56 km) radius of a lek. Conifer land cover was derived from Falkowski et al. (in press). The Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) is based on lek data from 1995 to 2015. Active, historic, and inactive leks are overlaid.



aURHNj —Partial dependence plot showing the predicted relationships among the proportion of sagebrush within a 120-m buffer and counts of Brewer's sparrow (BRSP), sagebrush sparrow (SASP), and sage thrasher (SATH) (Donnelly et al., in press). There is an apparent threshold value of 40 percent landscape cover of sagebrush above which abundance of the different species increases. The background histogram is the frequency of covariate values across the landscape and shows that a large proportion of sampled areas had low density of sagebrush (right y-axis).

Ecosystem Resilience and Resistance

Once suitable habitat for sage-grouse is identified, appropriate conservation and restoration actions are determined by assessing the likely ecological response to disturbances and management treatments. Soil temperature and moisture regimes can be used as indicators of resilience to disturbance and resistance to invasive annual species like cheatgrass in sagebrush ecosystems (Chambers et al. 2007; Chambers et al. 2014a,b,c; Maestas et al. 2016). In general, higher potential resilience and resistance occurs with ***cool*** to ***cold*** (frigid to cryic) soil temperature regimes and ***moist*** (udic), ***winter moist*** (xeric), or predominantly ***summer moist*** (ustic) soil moisture regimes, while lower potential resilience and resistance occur with ***warm*** (mesic) soil temperatures and relatively ***dry*** (aridic) or ***summer moist bordering on dry*** (ustic bordering on aridic) soil moisture regimes (figs. 21, 22; Chambers et al. 2014a,b; Maestas et al. 2016). An explanation of soil temperature and moisture regimes is in Appendix 2.

High soil moisture typically equates to elevated productivity and thus increased resilience (Chambers et al. 2014b), whereas cold soil temperatures typically limit growth and reproduction of nonnative invasive annual grasses and thus increase resistance (Chambers et al. 2007). The timing of precipitation also is important

because cheatgrass and many other invasive annual grasses are particularly well-adapted to climates with cool and wet winters and warm and dry summers (fig. 4; Bradford and Lauenroth 2006; Bradley 2009). In contrast, areas that receive regular and relatively abundant summer precipitation (ustic soil moisture regimes at the high end of the precipitation gradient) often are dominated by warm and/or cool season grasses (Sala et al. 1997). These grasses likely create a more competitive environment and result in greater resistance to annual grass invasion and spread (Bradford and Lauenroth 2006; Bradley 2009).

For this report, we describe the predominant sagebrush ecological types in relation to soil temperature and moisture regimes, typical vegetation, and resilience to disturbance and resistance to invasive annual grass (table 3). To facilitate landscape analyses and prioritization, we categorized relative resilience and resistance based on soil temperature regime and moisture regime subclasses (fig. 7) and the predominant sagebrush ecological types (table 3; Appendix 3). We assigned each soil temperature regime and moisture regime subclass to one of three categories of relative resilience and resistance: high, moderate, and low. An explanation of soil temperature and moisture regimes and cross-walks between soil temperature and moisture regimes and relative resilience and resistance are in Appendix 2. To facilitate assessments across scales, we developed state-and-transitions models for the predominant ecological types based on soil temperature and moisture regimes and relative resilience and resistance of the sagebrush ecosystem types (Appendix 6). State-and-transition models provide information on the alternative states, ranges of variability within states, and processes that cause plant community shifts within states as well as transitions among states.

Much of the West-Central Semiarid Prairies (Management Zone I) is characterized by moderate to high resilience and resistance as indicated by relatively cool and summer moist regimes (fig. 7; table 3). However, the southeastern part of this ecoregion has low to moderate resilience and resistance as indicated by warm (mesic) and drier regimes (ustic bordering on aridic) (table 3). The dominant ecological types are comprised of varying amounts of cool season and warm season grasses, Wyoming big sagebrush, and plains silver sagebrush (table 3). The Western Cordillera in Management Zones II and VII grades into the foothills of the Wyoming Basin and Colorado Plateau and is characterized by cold and wet to cool and summer moist soil temperature and moisture regimes with generally high to moderate resilience and resistance (fig. 7; table 3). Ecological types are typically comprised of mountain big sagebrush, snowberry, other shrubs, and cool season grasses (table 3). The Cold Deserts in Management Zones II and VII encompass a broad range of soil temperature and moisture regimes—cool bordering on cold and summer moist bordering on dry to warm and dry—with generally moderate to low resilience and resistance (fig. 7; table 3). The ecological types are characterized by mountain big sagebrush on the coolest sites, Wyoming big sagebrush and salt desert shrubs on the warmest and driest sites, and basin big sagebrush and sometimes silver sagebrush in drainages. Cool season grasses predominate with warm season grasses occurring in some types with summer moisture.

Table 3—Predominant sagebrush ecological types in the West-Central Semiarid Prairies (MZ I), Western Cordillera, and Cold Deserts Ecoregions (MZ II, VII) based on soil temperature and moisture regimes (to moisture subclass), typical characteristics, and resilience to disturbance and resistance to invasive annual grasses. Relative abundance of sagebrush species and composition of understory vegetation vary depending on major land resource area (MLRA) and ecological site type. Definitions of MLRAs, state-and-transition models, ecological types, and ecological sites are in Appendix 1. The methods used to determine the predominant ecological types and a map that intersects the MLRAs, ecoregions, and management zones are found in Appendix 3. State-and-transition models were developed for most of these ecological types for this report (Appendix 6). A detailed description of how to use this information is in the section on "Determining Appropriate Management Treatments at Local Scales" in this report.

Ecological Type	Characteristics	Resilience and Resistance
Cool bordering on cold/ Summer moist bordering on dry (Frigid bordering on Cryic/Ustic bordering on Aridic) Representative Area: Northwestern Glaciated Plains—MLRA 52 in northern Montana	Precipitation: 10-14 inches Typical Vegetation: *Green needlegrass, wheatgrasses, needle-and-thread, plains silver sagebrush* Grass dominated—cool with some warm season grasses	*Resilience*—High precipitation and high productivity result in high resilience. *Resistance*—Climate suitability to invasive annual bromes is low due to low soil temperature and club mosses.
Cool/Summer moist (Frigid/Ustic) Representative Area: Northwestern Great Plains—MLRA 60A in South Dakota	Precipitation: 13-18 inches Typical Vegetation: *Western wheatgrass, green needlegrass, blue and sideoats grama, buffalograss, plains silver sagebrush, Wyoming big sagebrush on shallow clay sites* Grass dominated—mixture of cool and warm season grasses	*Resilience*—**Moderate to high.** Effective moisture and productivity are high, depending on soil texture. *Resistance*—**Moderate to high**. Climate suitability to invasive annual grasses is moderate to high increasing on warmer sites.
Cool/Summer moist bordering on dry (Frigid/Ustic bordering on Aridic) Representative Area: Northwestern Great Plains—MLRA 58A in Montana and 58D in South Dakota, 58C in North Dakota	Precipitation: 10-14 inches Typical Vegetation: *Wyoming big sage, plains silver sage, wheatgrasses, green needlegrass, needle-and-thread, and blue grama* Shrub dominated—cool with some warm season grasses	*Resilience*—**Moderate to high.** Effective moisture and productivity are relatively high, depending on soil texture. *Resistance*—**Moderate to high**. Climate suitability to invasive annual grasses is minor and increases on warmer and drier sites.
Warm/Summer moist (Mesic/Ustic) Representative Area: Northwestern Great Plains—wetter portions of MLRA 58B in Wyoming near Black Hills	Precipitation: 15-17 inches Typical Vegetation: *Wyoming big sagebrush, western wheatgrass, green needlegrass, needle-and-thread* Ponderosa pine potential Shrub dominated—cool and warm season grasses	*Resilience*—**Moderate to high.** Effective precipitation and productivity are relatively high. *Resistance*—**Moderate**. Climate suitability to invasive annual grasses is moderate to low depending on soil temperature and texture.
Warm/Summer moist bordering on dry (Mesic/Ustic bordering on Aridic) Representative Area: Northwestern Great Plains—drier portions of MLRA 58B in Wyoming, and probably warmer portions of 58A, Land Resource Unit E in southeastern Montana	Precipitation: 10-14 inches Typical Vegetation: *Wyoming big sagebrush, silver sagebrush, wheatgrasses, green needlegrass, needle-and-thread, blue grama* Shrub dominated—cool and warm season grasses	*Resilience*—**Low to moderate.** Effective precipitation and productivity are relatively low. *Resistance*—**Low to moderate**. Climate suitability to invasive annual grasses is moderate to high depending on soil temperature and texture.

Table 3—(Continued)

R□wl4WdP4JLEE.45fLJJE.5WJEP(lk4WlP,yL□w□

Ecological Type	Characteristics	Resilience and Resistance
Cold/Wet (Cryic/Udic) Representative Area: Middle and Southern Rockies—MLRA 43B in Wyoming and Montana; 48A in Colorado; MLRA 47 in Utah **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 20+ inches Typical Vegetation: *mountain big sagebrush, spiked big sagebrush, snowberry, mountain silver sagebrush , aspen, lodgepole pine, slender wheatgrass, fescues, needlegrasses, bromes* Shrub dominated—cool season bunchgrasses	*Resilience*—DLBk□High precipitation and high productivity result in high resilience. *Resistance*—DLBk□Climate suitability to invasive annual bromes is low due to low soil temperature.
Cold/Summer moist (Cryic/Ustic) Representative Area: Middle and Southern Rockies—MLRAs 46/43B Foothills in Wyoming and Montana; MLRA 48A in Wyoming and Northern Colorado; MLRA 49 in Wyoming **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 15-19 inches Typical Vegetation: *mountain big sagebrush, bitterbrush, snowberry, serviceberry, mahogany, aspen, fescues, needlegrasses, bluebunch wheatgrass* Shrub dominated—cool season bunchgrasses	*Resilience*—DLBk□High precipitation and high productivity result in high resilience. *Resistance*—DLBk□Climate suitability to invasive annual bromes is low due to low soil temperature. High variability due to aspect with lower resistance on south-facing aspects.
Cool/Summer moist (Frigid/Ustic) Representative Area: Uinta Mountains (MLRA 47, LRU C) in Utah and Wyoming; Southern Rockies in Colorado and Utah—MLRA 48A **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 16-22 inches Typical Vegetation: *mountain big sagebrush, serviceberry, snowberry, bitterbrush, western wheatgrass, needlegrasses, bluegrasses* Shrub dominated—cool season grasses with some warm season grasses in southern extent	*Resilience*—**Moderate to high.** Precipitation and productivity are moderate. Decreases in herbaceous perennial species, and ecological conditions can decrease resilience. *Resistance*—**Moderate to high.** Climate suitability to invasive annual grasses is relatively high.
Cool/Winter moist (Frigid/Xeric) Described in Chambers et al. 2014b. Representative Area: Wasatch and Uinta Mountains in Utah (MLRA 47)	Precipitation: 12-22 inches Typical vegetation: m*ountain big sagebrush, antelope bitterbrush, snowberry, or low sagebrush, bluebunch wheatgrass, basin wildrye, Nevada bluegrass* Piñon pine and juniper potential in some areas Shrub dominated—cool season grasses	*Resilience* – **Moderately high**. Precipitation and productivity are generally high. Decreases in site productivity, herbaceous perennial species, and ecological conditions can decrease resilience. *Resistance*—**Moderate**. Climate suitability to invasive annual grasses is moderate, but increases as soil temperatures increase.

dPEJ□w.4IwRZPHLWBe5wLW5WJdPEP45JPcE5I.5(□

Ecological Type	Characteristics	Resilience and Resistance
Cool/Summer moist bordering on dry (Frigid/Ustic bordering on Aridic) Representative Area: Wyoming Basin—MLRA 34A in Wyoming east of continental divide and southern extent of MLRA 34A in Colorado west of continental divide. **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 10-14 inches Typical Vegetation: *Wyoming big sagebrush; basin big sagebrush or silver sagebrush in drainages, wheatgrasses, needle-and-thread, Indian ricegrass* Shrub dominated—cool season grasses with some warm season grasses (blue grama)	*Resilience*—**Moderate**. Precipitation and productivity are moderate. Decreases in site productivity, herbaceous perennial species and ecological conditions can decrease resilience. *Resistance*—**Moderate.** Climate suitability to invasive annual bromes is relatively low, but increases with temperature and soil sand content.

Table 3—(Continued)

dPEJ□w.4IwRZPHLWBe5wLW5WJdPEP45JPcE5I.5(□

Ecological Type	Characteristics	Resilience and Resistance
Cool bordering on warm/ Summer moist (Frigid bordering on Mesic/Ustic) Representative Area: Colorado Plateau – MLRA 48A/34A Piceance Basin-Book Cliffs in Colorado and Utah **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 14-18 inches Typical Vegetation: *Wyoming big sagebrush, basin big sagebrush in drainages, mountain big sagebrush, Utah juniper, twoneedle pinyon, Gambel oak, basin wildrye, rhizomatous wheatgrasses, Sandberg bluegrass* Pinyon-juniper potential Shrub dominated—cool with some warm season grasses	*Resilience*—**Moderate to high.** Effective precipitation and productivity are high, depending on soil texture. Erosive soils and steep terrain can decrease resilience. *Resistance*—**Moderate to Low**. Climate suitability to invasive annual grasses is moderate. Decreases in site productivity, herbaceous perennial species, and ecological conditions decrease resistance.
Cool/dry bordering on summer moist (Frigid/Aridic bordering on Ustic) Representative Area: Wyoming Basin – MLRA 34A in Green River Basin (west of continental divide) and Great Divide Basin	Precipitation: 7-10 inches Typical Vegetation: *Wyoming big sagebrush and salt desert shrubs, bottlebrush squirreltail, needleandthread, Indian ricegrass, wheatgrasses* Shrub dominated—cool season grasses	*Resilience*—**Moderate to Low**. Effective precipitation limits site productivity. Decreases in productivity, perennial herbs, and ecological conditions further decrease resilience. *Resistance*—**Moderate.** Climate suitability to invasive annual grasses is moderate, but depends on soil texture and temperature.
Warm/summer moist bordering on dry (Mesic/Ustic bordering on Aridic) Representative Area: Wyoming Basin – MLRA 32 foothills in Wyoming, MLRA 34B and 36 in Colorado and Utah **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 10-14 inches in Wyoming; 12-16 inches in Utah and Colorado Typical Vegetation: *Wyoming big sagebrush, Utah juniper and twoneedle pinyon, wheatgrasses, needleandthread, Indian ricegrass* Shrub dominated—cool season grasses with warm season grasses increasing in the south	*Resilience*—**Moderate to low.** Effective precipitation and productivity are moderately low, and vary with soil temperature and texture. *Resistance*—**Low**. High climate suitability to invasive annuals.
Warm/Dry bordering on summer moist (Mesic/Aridic bordering on Ustic) Representative Area: Wyoming Basin and Colorado Plateau—MLRAs 32 foothills in Wyoming and MLRA 34B and36 in Colorado and Utah **Applies to both Gunnison and Greater sage-grouse habitats**	Precipitation: 8-12 inches Typical Vegetation: *Wyoming big sagebrush, fourwing saltbush, Utah juniper, black sagebrush, shadscale, needleandthread, Indian ricegrass, wheatgrasses, galleta,* Shrub dominated—cool season grasses with some warm season grasses	*Resilience*—**Moderate to low.** Effective precipitation and productivity are moderately low, and vary with soil temperature and texture. *Resistance*—**Low.** Climate suitability to invasive annuals is high. Decreases in site productivity, herbaceous perennial species, and ecological conditions decrease resistance.
Warm/Dry (Mesic/Aridic) Representative Area: Wyoming Basin—MLRA 32 in Wyoming (Bighorn and Wind River Basins)	Precipitation: 5-9 inches Typical Vegetation: *Wyoming big sagebrush, salt desert shrubs, wheatgrasses, needleandthread, Indian ricegrass* Shrub dominated—cool season grasses with some warm season grasses	*Resilience*—**Low.** Effective precipitation and productivity are low resulting in low resilience. *Resistance*—**Low.** Climate suitability to invasive annual grasses is high. Decreases in site productivity, herbaceous perennial species, and ecological conditions decrease resistance.

Knowledge of the potential resilience and resistance of sagebrush ecosystems can be linked with the probability that an area will provide sage-grouse breeding habitat to determine priority areas for management and identify effective management strategies (Chambers et al. 2014a; Wisdom and Chambers 2009). The sage-grouse habitat matrix (table 4) illustrates an area's relative resilience to disturbance and resistance to invasive annual grasses in relation to its probability of providing habitat for sage-grouse. As resilience and resistance go from high to low, timeframes required for sagebrush regeneration and perennial grass and forb abundance progressively limit the capacity of sagebrush ecosystems to recover after disturbances without management assistance. The risk of annual invasives increases and the ability to successfully restore burned or otherwise disturbed areas decrease as resilience and resistance decrease. As the probability of sage-grouse breeding habitat goes from low to high within these same ecosystems, the capacity to sustain populations of sage-grouse increases. Areas with breeding habitat probabilities of 0.25 to less than 0.5 are unlikely to provide adequate breeding habitat for sage-grouse. Areas with breeding habitat probabilities of 0.5 to less than 0.75 can provide breeding habitat for sage-grouse, but are at risk if sagebrush loss occurs without recovery or if other factors negatively impact the area, such as conifer expansion, development, or infrastructure. Areas with breeding habitat probabilities greater than or equal to 0.75 can provide the necessary breeding habitat conditions for sage-grouse to persist.

Management strategies can be determined by considering (1) resilience to disturbance and resistance to nonnative invasive plants, (2) sage-grouse breeding habitat probabilities, and (3) the predominant threats to both sagebrush ecosystems and their associated sage-grouse populations. Management strategies for the West-Central Semiarid Prairies (Management Zone I), Cold Deserts (Management Zone II), and Western Cordillera Ecoregions (Management Zone VII) are found in table 5. Because management strategies often cross-cut multiple program areas for land management agencies, an integrated approach is typically used to address the predominant threats. For example, agency program areas such as invasive plant management, fuels management, range management, and wildlife, may all contribute to vegetation management strategies designed to address persistent ecosystem and land use and development threats.

The sage-grouse habitat matrix is a decision support tool that allows land managers to better evaluate risks and decide where to focus specific activities to promote desired species and ecosystem conditions (table 4; Chambers et al. 2014a). Areas with high sage-grouse breeding habitat probabilities and high concentrations of birds are typically comprised of intact habitats and thus are high priorities for management (table 4 cells 1C, 2C, 3C). Protective management can be used in and adjacent to these areas to maintain habitat connectivity and ecosystem resilience and resistance. A diverse set of strategies can be used for protective management such as reducing or eliminating disturbances from land uses and development, establishing conservation easements, utilizing an early detection and rapid response approach (EDRR; USDI 2016) to invasive plant species management, or suppressing fires (table 5). Areas with high sage-grouse breeding habitat probabilities but lower resilience and resistance are slower to recover following fire and surface disturbances and are more susceptible to invasive plant species than areas with higher resilience and resistance (Chambers et al. 2014c).

G5CE□□—Sage-grouse habitat resilience and resistance matrix based on resilience and resistance concepts from Chambers et al. (2014a,b), and breeding habitat probabilities based on Doherty et al. (2016) for Greater sage-grouse and developed in this report for Gunnison sage-grouse. Rows show the ecosystem's relative resilience to disturbance and resistance to invasive annual grasses (1 = high resilience and resistance; 2 = moderate resilience and resistance; 3 = low resilience and resistance). Resilience and resistance categories were derived from soil temperature and moisture regimes (see Appendix 2; Maestas et al. 2016) and relate to the sagebrush ecological types in table 3. Columns show the landscape-scale sage-grouse breeding habitat probability based on table 1 (A = 0.25 to <0.5 probability; B = 0.5 to <0.75 O4PC5CLELIZdO4PC5CLELIZTw□□□

G5CE —Management strategies for persistent ecosystem threats, land use and development threats, and climate change in the West-Central Semiarid Prairies (MZ I), Western Cordillera, and Cold Deserts (MZ II and VII). Recommendations are provided for prioritizing and targeting strategies based on cells in the sage-grouse habitat resilience and resistance matrix (table 4). Threats and strategies are cross-cutting and affect multiple program areas. While many of these fall under the broad umbrella of vegetation management, an integrated approach will likely be used in addressing threats. For example, it is expected that multiple agency program areas such as invasive plant management, fuels management, range management, wildlife, and others will contribute to strategies that use vegetation manipulation to address persistent ecosystem and land use and development threats.

Gk4.5IAPWW5IL)pW)5wL).FO.,L.w

Management Strategies

- Use resilience and resistance categories and knowledge of invasive plant distributions to select appropriate management approaches.
  - Protect high quality (relatively weed-free) sagebrush communities with moderate-to-high sage-grouse habitat probabilities (cells 1B, 1C, 2B, 2C, 3B, 3C):
    - Focus on preventing introduction and establishment of invasive species, especially in low resistance areas with high susceptibility to annual grass invasion (in and adjacent to cells 3B, 3C).
    - Avoid seeding introduced forage species (crested wheatgrass, smooth C4PH.IL.WOPwl4l4k5CLELI5ILPWP44wlP45ILPWLWHPJ4BkLBk4wLE-ience and resistance areas because these species can dominate sagebrush communities.
    - Practice early detection-rapid response (EDRR) approaches for emerging invasive species of concern (in and adjacent to cells 1B, 1C, 2B, 2C, 3B, 3C).
  - Where weed populations already exist, seek opportunities to maximize treatment effectiveness by prioritizing restoration within relatively intact sagebrush communities (cells 1B, 1C, 2B, 2C, 3B, 3C). Restoration will likely be easier at locations in cooler and moister ecological types with higher resilience and resistance.
    - c4LP4LILN.wLLwxLIkw(;.LWlW5IL).O.4WWL5Ek4C5;.P(ww)O.wlP4wOPWJ to release from invasive plant competition.
    - Manage grazing to reduce invasive species and promote native perennial grasses. In the West-Central Semiarid Prairies and other cool and moist areas, manage grazing to reduce crested wheatgrass, Kentucky bluegrass, smooth brome, and other introduced forage species and to promote native cool season perennial grasses (see grazing strategies.
    - Attempt proactive management of invasive annual grasses in the understory P;w5B.C4(wkwl5WJwlP4J(;xLEJ4l4Lwyxk.4.O4P).WH.IkPJ wzLwl45Ik-4Ik5W.P;(wLWB;;P4lwz;E(wL).EZPWOPwl4l5WW(5EB45ww;PWl4PELwl4L;l spread of large weed infestations located in lower habitat probability areas (cells 1A, 2A, 3A) to prevent compromising adjacent higher quality habitats (cells 1B, 1C, 2B, 2C, 3B, 3C).

Gk4.5IdPWL;.4SzO5WwLPW

Management Strategies

- Addressing conifer expansion requires an interdisciplinary approach and necessarily involves multiple program areas.
  - Apply integrated vegetation management practices to treat conifer expansion, using an interdisciplinary approach in designing projects and treatments.
  - Focus tree removal on early to mid-phase (e.g., Phases I, II) conifer expansion into sagebrush ecological sites to maintain shrub/herbaceous cover.
  - 1B, 2A, 2B) to control conifer expansion.
  - Prioritize for treatment:

- Areas with habitat characteristics that can support sage-grouse with moderate to high resilience and resistance (cells 1B, 1C, 2B, 2C), especially near leks. (Note: cells 3B and 3C are generally too warm and dry to support conifers.).
- Areas where conifer removal will provide connectivity between sagebrush habitats.
- t4.5wxk.4w(,jL.WIO.4.WWL5EB45ww.w5WJ,P4Cw.zLwIIPO4PHPl.4,P).4Z

Gk4.5IRLEJ4.

Management strategies

EB2p-1p2U3B#,w Protection of areas supporting sagebrush is important for maintaining sage-grouse habitat. The West-Central Semiarid Prairies (MZ I) have limited availability of sagebrush and all areas with moderate and especially low resilience and resistance have longer recovery periods. If resources become limiting, consider the following prioritization:

- Fire suppression typically shifts from low to moderate priority when resistance and resilLW,.5IBP4L.wwkL,.I,4PHkLBkIPHPJ.45I.C(I.I)54L.wxLI kE54B.4.4Lwy5WJE5WJ scape condition (cells 1B, 1C, 2B, 2C). In low resistance and resilience areas, the priority shifts from moderate to high as sage-grouse habitat probability increases (cell 3B, 3C). Scenarios requiring high priority may include:
  - Areas of sagebrush that bridge large, contiguous expanses of sagebrush and that are important for providing connectivity for sage-grouse.
  - Areas where sagebrush communities have been successfully reestablished through seedings or other rehabilitation investments.
  - Fire Potential products; National Weather Service Fire Weather Watches and Red aE5BR54WLWBw5WJ.4.C.k5)LP45W5EZw.w5WJEP,5E4.W)L4PWH.WIPCw.4)5ILPWw.

a(.Ewf5W5B.H.WI. a(.EwH5W5B.H.WILW,E(J.w)B.I5ILPWO4PK.,lwlk5IHLILB5I.xLB4. risk, improve resilience to disturbance, and restore habitat, as well as actions intended to protect intact sage-grouse habitat. Mechanical treatments are typically applied to reduce fuel loading or to alter species composition consistent with Land Use Plan objectives. Prescribed 4LwPW.,P4HP,;(.EwH5W5B.H.WIlk5IH5ZC.(w.JIPLHO4P) k5CLI5I,PWJLILPWwP4,4. 5I.,(.E,PWJLILPWwlk5IELHLI,(l(4.4wO4.5JLW54.5wxLIk HPJ.45I.IPkLBk4.wLEL.W,.5WJ. resistance, but should be considered only after consultation with local biologists and land managers. Chemical and seeding treatments are conducted to reduce invasive species and IP,k5WB.wO.,L.w,PHOPwLILPWIPW5IL).5WJP4HP4.4.4wLwl5WIwO.,L.wxk.4.W5IL). perennial grasses and forbs are depleted. When setting priorities for fuels management, consider the following.

<u>Mechanical Treatments</u>

- Mechanical treatments conducted to minimize sagebrush loss (e.g., conifer reduction) is a high priority in areas with high breeding habitat probabilities and moderate to high resilience and resistance (cells 1B, 1C, 2B, 2C), and shifts to low in areas with low breeding habitat probabilities (cells 1A and 2A).
- In areas of low resilience and resistance, mechanical treatments to minimize sagebrush loss shifts in priority from low to high as the sage-grouse habitat probability increases (cells 3B, 3C). However, treatments intended to decrease fuel loads and increase perenWL5Ek4C5,P(wwO.,L.wH5ZC.L.W.,,,IL).L,LWw(,jL.WIO.4.WWL5EB45ww.w5WJ,P4Cw. exist to promote recovery and resist invasive plant species.
- Management activities may include:
  - Tree removal in early to mid-phase (Phases I, II) post-settlement conifers to maintain shrub/herbaceous cover and reduce fuel loads.
  - Removal of mountain shrub species that encroach into sagebrush communities (e.g., gambel oak, curlleaf mountain mahogany, snowberry, serviceberry.)
  - Tree removal in later phase (Phase III) post-settlement conifers to reduce risks or E54B.P4kLBkw.).4LIZ4.w.
  - Herbicide and/or seeding associated with mechanical treatments to reduce invasive wO.,L.w5WJ.4.wIP4.W5IL).O.4.WWL5EwO.,L.wLW54.5wxLIkLW.)wW5IL).O.4.W - nial grasses and forbs for recovery.

G5CE□□—(Continued).

Prescribed Fire

□ dPWwLJ.45EI.4W5IL).wIPO4w,4LC.J4xk.4Plk4I4.5IH.WI5 EI.4W5IL).wH5ZH.1□ management objectives.

□ pWEPx4wLEL.W,.5WJ4wLwI5W,.54.5w,PWwLJ.4O4w,4LC.J4WEZ5;.4,PWw(EI5ILPW□ with local biologists and land managers and when:

- o □ □ trajectory will lead to functioning sagebrush communities. Most low resilience and resistance areas that receive <12 in (30.5 cm) of precipitation do not respond favorably to burning.
- o Burning is part of multi-stage restoration projects where burning is required to remove biomass following chemical treatments for site preparation.
- o Monitoring data validates that the preburn composition will lead to successful, native plant dominance postburn.

□ TwO4w,4LC.J4w.E,IL)EZLWHPJ.45IIPkLBk4wLELW,.5 WJ4wLwI5W,.54.5w5;.4□ consultation with local biologists and land managers and assessing site recovery potential and other management options based on the following:

- o Preburn community composition.
- o Probability of invasive species establishment.
- o □ □
- o □ □
- o Alternative treatments that may meet objectives.

□ c4w,4LC.J4.5,IL)LIL.wH5ZLW,E(J□

- o Burning piles or concentrations of woody biomass resulting from mechanical treatments.
- o Broadcast burning in areas having conifer concentrations that interface with sagebrush communities, while intentionally avoiding burning intact sagebrush that is not 4IIPE.45WI□
- o □
- o □ □ suppression.
- o □ □ - cies composition.

Chemical Treatment and Seeding: Herbicide treatments and seedings are used to decrease invasive species composition and increase native species dominance where perenWL5EW5IL).B45ww.w5WJ.P4Cw54.LWw(;.L.WI.P4wLI.4,P).4ZD.4CL,LJ.I4.5IH.WIwH5ZC.□ w.E,IL).EZ5OOEL.JLW.PWK(W,ILPWxLIkO4.w,4LC.J4.P4H.,M5L,5EI4.5IH.WIwGZOL,5EEZ□ these treatments are in response to clear evidence of a nonnative invasive species threat.

cPwI4.4k5CLELI5ILPW□ cPwI4.4k5CLELI5ILPWLw5.4Pww.(IILWB.;.P4ILW)PE).LWB45WB.xLEJ EL.;.wPLEw4.5WJ.(.Eww(CK.,IH5II.4.zO.4ILw.s.W.45E□ .,PWwLJ.45ILPWw.P4O4LP4.LILN5ILPWP;□ OPwI4.4k5CLELI5ILPW.;.P4Iw54.□

- □ Priority shifts from generally low priority (cells 1A, 2A, 3A, 1B, and 1C) to moderate priority in moderate resilience and resistance areas (cells 2B, 2C). Areas of low resilience/resistance shift in priority from low priority to high priority with increasing habitat probability for sage-grouse (cells 3B to 3C).
- □ Areas of higher priority include:
  - o Areas where perennial herbaceous cover, density, and species composition is inadequate for recovery.
  - o Areas where seeding or transplanting sagebrush is needed to maintain habitat connectivity for sage-grouse.
  - o Areas threatened by nonnative invasive plants.
  - o Steep slopes and soils with erosion potential.

Gk4.5dELH5I.dk5WB.□

Management strategies

□ Where effects of climate change and its interactions with stressors are expected to be relatively small and knowledge and capacity high, continue to use best management practices.

G5CE□□—(Continued).

- □ Where climate change and stress interactions are expected to be severe, proactive management such as assisted migration may be necessary to facilitate transition to a new site potential.
- □ Practice drought adaption measures such as reduced grazing during droughts, conservation actions to facilitate species persistence, and seeding and transplanting techniques proven to work during drought.
- □ Use species and ecotypes for seeding and out-planting that are adapted to both site conditions and drought, and resilient to episodic drought where projections indicate long-term climate change.
- □ Monitor transition zones between climatic regimes (the edges). Plant community shifts that affect management decisions often occur between Major Land Resource Areas or Level III Ecoregions.

Gk4 5B45NLWB

Management strategies

- □ Manage livestock grazing to maintain a balance of perennial native grasses (warm and/or cool season species as described in ESDs for that area), forbs, and biological soil crusts to allow natural regeneration and to maintain resilience. Ensure strategies prevent degradation and loss of native cool-season grasses in particular. Areas with low to moderate resilience and resistance may be particularly vulnerable (cells 2A, 2B, 2C, 3A, 3B, 3C).
- □ Implement grazing strategies that incorporate periodic rest during the critical growth period, especially for cool season grasses, to ensure maintenance of a mixture of native perennial grasses. This strategy is important across all sites, but particularly essential on areas with low to moderate resilience and resistance supporting sage-grouse habitat (cells 2B, 2C, 3B, 3C).
- □ Ensure grazing strategies are designed to promote native plant communities and decrease nonnative invasive species. In ephemeral drainages and higher precipitation areas in the West-Central Semiarid Prairies that receive more summer moisture and have populations of nonnative invasive plant species, too much rest may inadvertently ;5)P4wO,Lww(,k5wEJC4PH.m.WI(,yZCE(,B45ww5WJwHPPI kC4PH.tJK(wIH.Wlw in timing, duration, and intensity of grazing may be needed to reduce these species.

Gk4 5ISW 4BZ)EPOH.WI

Management strategies

- □ Avoid development, if feasible, in areas with high breeding habitat probability for sage-grouse and high sagebrush cover (cells 1C, 2C, 3C) and steer development in non-habitat areas (1A, 2A, 3A).
- □ Minimize habitat fragmentation in areas with moderate and high breeding habitat probabilities for sage-grouse (cells 1B, 2B, 3B, 1C, 2C, 3C).
- □ For disturbances that remove vegetation and cause soil disturbance, minimize and miti- B5I□HO5,IwIPOwPLEC5WyLWB,4IJx,J,4,1LW,E(JLWB5WW(5EC4PH.wvw.JHLzw appropriate seeding technologies, and monitoring). Plan for multiple restoration interventions in areas with low resilience and resistance (cells 3B, 3C).
- □ Minimize energy transport corridors (e.g., roads, pipelines, transmission lines) and limit vehicle access, where feasible.
- □ Maintain resilience and resistance of existing patches of sagebrush habitat by aggressively managing weeds that may require the following management practices (especially important in low resilience and resistant areas—cells 3A, 3B, 3C):
  - o □ area
  - o □ □
  - o Assessing and treating weed populations, if necessary, prior to surface disturbing activities
  - o Removing mud, dirt, and plant parts from construction equipment
  - o Addressing weed risk and spread factors in travel management plans
  - o Ensuring timely establishment of desired native plant species on reclamation sites
  - o Using locally adapted native seed, if possible

G5CE□□—(Continued).

- Intensively monitoring reclamation sites to ensure seeding success and to determine presence of weeds
- Using mulch, soil amendments, or other practices to expedite reclamation success when necessary
- Ensuring weeds are controlled on stockpiled topsoil.

Gk4□5IT4C5W5WJSz(4C5W□)□EPOH□Wl□

Management strategies

□ Secure conservation easements to maintain existing sagebrush stands and sage-grouse habitat. Prioritize areas with high habitat probability for sage-grouse and high sagebrush cover (cells 1C, 2C, 3C).

□ Encourage the protection of existing sage grouse habitat through appropriate land use planning and Federal land sale policies. Steer development towards non-habitat (cells 1A, 2A, 3A) where habitat is unlikely to become suitable through management.

Gk4□5Id4POE5WJdPW)□4wLPW

Management strategies

□ Secure conservation easements to maintain existing sagebrush grasslands and sage-grouse habitat and prevent conversion to tillage agriculture. Prioritize all areas supporting moderate-to-high sage-grouse habitat probability (cells 1B, 1C, 2B, 2C, 3B, 3C) in locations where tillage risk is elevated (see Sage Grouse Initiative Cultivation Risk layer).

□ Secure term leases (e.g., 30 years) to maintain existing sagebrush grasslands and sage-grouse habitat and prevent conversion to tillage agriculture as a secondary strategy to conservation easements. Prioritize all areas supporting moderate-to-high sage-grouse habitat probability (cells 1B, 1C, 2B, 2C, 3B, 3C) especially in locations where tillage risk is elevated (see Sage Grouse Initiative Cultivation Risk layer).

□ Offer alternatives to farming on expired USDA Conservation Reserve Program lands through Federal and state programs. Prioritize lands in and around intact habitats (cells 1B, 1C, 2B, 2C, 3B, 3C).

□ Encourage enrollment in the USDA Conservation Reserve Program to return tilled lands to perennial plant communities supporting mixtures of grasses, forbs, and sagebrush xk4□Ik4□54□C□W□IwIPw5B□B4P(w□c4LP4LILN□E5WJwLW5WJ□54P(WJLWI5,Ik5CLI5Iw□ (cells 1B, 1C, 2B, 2C, 3B, 3C).

Gk4□5IE5B□C4(wkI□J(,IL□PW

Management strategies

□ ***s#BuB,3p,3B#,UNwUHpb2ñwF2pO#UN12pwx2Bbpu2pxFpOBxUN#2OpxFU,BxUN2pO#UN***□ across all areas in the West-Central Semiarid Prairies due to relatively limited sagebrush availability and extended periods of recovery in the region. Many areas are characterized by moderate to moderately low resilience and resistance, and many sagebrush species lack the capacity to resprout.

□ Use caution when attempting to increase herbaceous perennials by reducing sagebrush dominance through mechanical or chemical treatments in general.
  - Lower resistance and resilience areas are prone to annual grass increases and potential dominance if annual grasses exist in the area before treatment.
  - Pretreatment densities of 2 to 3 native perennial bunch grasses per square meter are often necessary for successful increases in perennial herbaceous plants and for suppression of annual grasses after treatment in lower resistance and resilience areas (Miller et al. 2014, 2015).

Consequently, these low resilience and resistance areas are at greater risk of habitat loss than areas with moderate to high resilience and resistance and are among the highest priorities for protective management (table 4 cell 3C; Chambers et al. 2014c).

Areas with moderate sage-grouse breeding habitat probabilities are comprised of habitat that supported a higher proportion of leks in the past than currently (table 2) and that may be improved through various management strategies (table 4 cells 1B, 2B, 3B). Management objectives may include increasing resilience and resistance by promoting perennial grasses and forbs through conifer removal or improved livestock management, reducing or eliminating new infestations of invasive plants through EDDR approaches, or restoring sagebrush habitat through seeding or transplanting (table 5). Management strategies often have synergistic effects. Increasing native perennial grasses and forbs can decrease the probability of invasion or expansion of annual invasive grasses (Chambers et al. 2007; Reisner et al. 2013) and, in turn, reduce the risk of altered fire regimes, transitions to undesired states, and decreased connectivity. Similarly, management strategies aimed at reducing the risk of wildfires outside of the historical range of variation, such as removing conifers in expansion areas, can increase the functional capacity of plant communities to resist invasive annual grasses (Chambers et al. 2014b) as well as enhance habitat connectivity (Baruch-Mordo et al. 2013).

The relative resilience and resistance of an area strongly influences its response to management strategies such as conifer removal or post-fire rehabilitation and the likelihood of nonnative annual grass invasion (Chambers et al. 2014b; Miller et al. 2013, 2014, 2015). Areas with lower resilience and resistance may still be among the highest priorities for management in areas with moderate breeding habitat probabilities, but they may require greater investment and repeated interventions to achieve management objectives (table 4 cell 3B; Chambers et al. 2014a).

Areas with low sage-grouse breeding habitat probabilities are characterized by habitat that supported active sage-grouse leks in the past, but that currently support few leks (table 4 cells 1A, 2A, 3A). If land use and development threats such as oil and gas development or cropland conversion are causing low sage-grouse breeding habitat probabilities, then habitat improvement may not be feasible. However, if the area has the capacity to respond to management treatments and if breeding populations are close enough for recolonization, improvement of these areas to increase breeding habitat probabilities may still be possible. Managers may decide to restore critical habitat in these types of areas, but the degree of difficulty and time frame required for habitat restoration increase as resilience and resistance decrease (Chambers et al. 2014a,c). Consequently, substantial investment and repeated interventions may be required to achieve objectives.

Careful assessment of the area of concern will always be necessary to determine the relevance of a particular strategy or treatment because sagebrush ecosystems occur over continuums of environmental conditions, such as soil temperature and moisture, and have differing land use histories and species composition (Miller et al. 2014, 2015; Pyke et al. 2015a,b). Also, areas with low sage-grouse breeding habitat probabilities may support other resource values or at-risk species (Rowland et al. 2006) that could benefit from management strategies designed to improve habitat. Knowledge of the locations of other priority resources and at-risk species and their response to management treatments can help ensure that treatments are located and strategies are implemented in a manner that will also benefit these other resources and species.

Intervention at the Ecoregional/Management Zone Scale

Effective management and restoration of sage-grouse habitat prioritizes the best management practices in the most appropriate places. This section describes an approach for targeting areas for sage-grouse habitat management based on widely available data, including (1) Priority Areas for Conservation for GRSG and critical habitat and linkages for GUSG, (2) breeding habitat probabilities and population indices, (3) ecosystem resilience and resistance, and (4) persistent ecosystem and land use and development threats. Here, key data layers are identified, the steps used to overlay and analyze the various data layers are discussed, and interpretations of the maps and analyses are provided. Datasets used to conduct the analyses and create the maps are in Appendix 4.

Priority Areas for Conservation and Critical Habitat

Sage-grouse priority areas for conservation have been delineated using available habitat and population data to identify areas critical for conserving GRSG populations (USFWS 2013). Similarly, critical habitat has been delineated for conserving GUSG populations (GSGRSC 2005; USFWS 2014a). These areas can be used as a first filter in prioritizing management actions. Habitats outside of priority areas for conservation and critical habitat areas are also important to consider where they provide genetic and habitat linkages and capture important seasonal habitats (USFWS 2013).

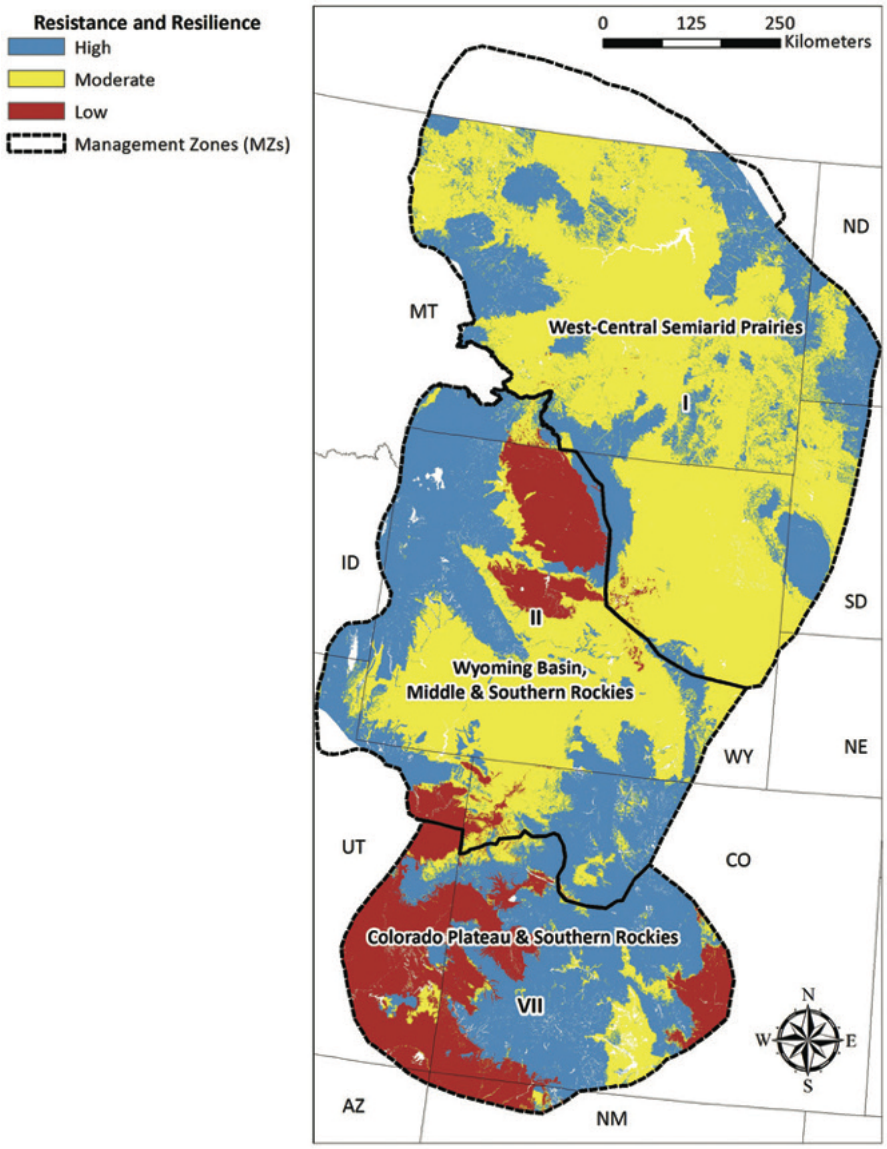
Breeding Habitat Probabilities and Population Indices

Further prioritization can be achieved by mapping areas with high breeding habitat probabilities and population indices. The breeding habitat models provide information on habitat characteristics (figs. 23, 24; table 1; Doherty et al. 2016). The categorical break points show the proportion of active and inactive leks in each sage-grouse Management Zone for GRSG and GUSG (table 2). These areas can be used to prioritize areas for management based on the probability of an area providing suitable habitat. The categorized breeding habitat probabilities overlaid with lek locations shows the relationship of modeled breeding habitat and active breeding locations (figs. 23, 24).

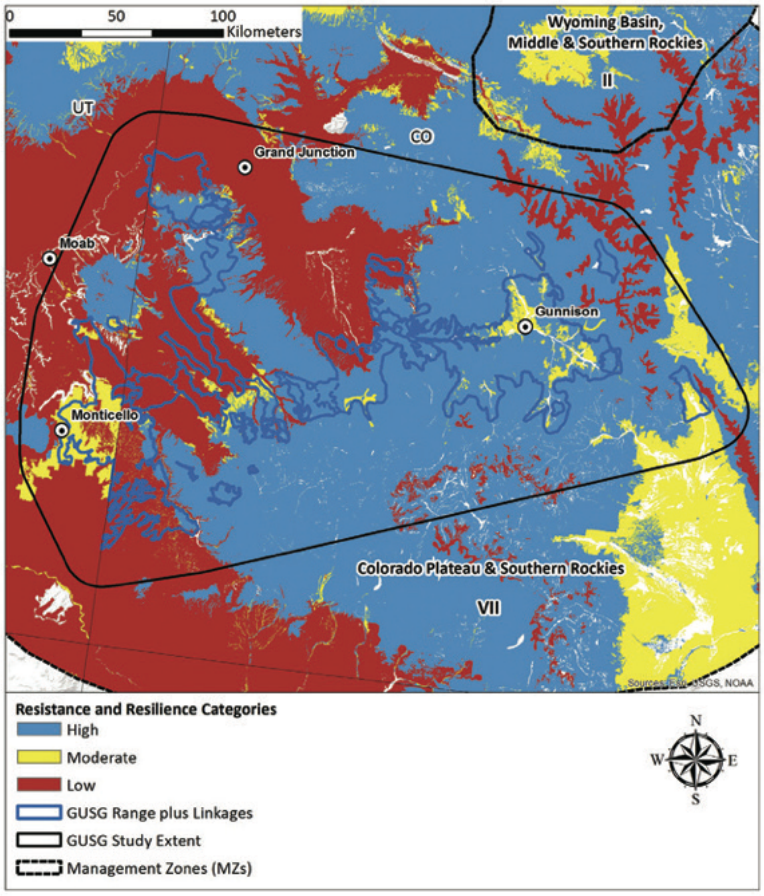
The population index model combines information from the breeding habitat model with lek count data to provide indices and spatial depictions of GRSG relative abundance (fig. 9; Doherty et al. 2016). Because the output of the population index model is a continuous surface or map, it can be used to focus conservation efforts on specified portions of sage-grouse populations identified by stakeholders (e.g., highest 25 percent or 85 percent of the population). For the purposes of this report, the population index model was classified into two categories (0–80 percent and 80–100 percent of the relative population). Because of the large area currently occupied by GRSG, the population index model can be used to better focus appropriate management actions on areas that: (1) currently support viable populations, (2) provide connectivity between population centers, and (3) occur close enough to breeding concentration areas to allow successful recolonization of reclaimed habitat (Coates et al. 2016).

Resilience to Disturbance and Resistance to Nonnative Invasive Annual Grasses

Resilience and resistance predictions coupled with sage-grouse breeding habitat probabilities and population indices provide critical information for determining areas for targeted management actions (table 5). Soil temperature and moisture regimes are strong indicators of ecological types as well as resilience to disturbance and resistance to nonnative invasive annual grasses figs. 7, 21, 22; table 3). The available data for soil temperature and moisture regimes were recently compiled for the western and eastern ranges of sage-grouse (Maestas et al. 2016; Appendix 2). Relative resilience and resistance categories were assigned to each soil temperature and soil moisture subclass to create a simplified index (table 3; figs. 28, 29;



aURHNj□—The soil temperature and moisture regimes categorized according to high, moderate, and low resilience and resistance in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.



—The soil temperature and moisture regimes categorized according to low, moderate, and high resilience and resistance in the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) and surrounding area. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.

Appendix 2) that allows managers to predict the ecological responses of sagebrush ecosystems to both disturbance and management actions.

Habitat Threats

Assessing the magnitude of persistent ecosystem and land use and development threats can provide important insights into targeting areas for treatment and the most appropriate management strategies (e.g., Hanser et al. 2011). Although habitat threats are considered in the breeding habitat and population index models (Doherty et al. 2016), depicting threats to different populations is necessary to assess their magnitude and evaluate viable management strategies. The threats and data sources considered in this report largely follow those in the Interagency Greater Sage-Grouse Disturbance and Monitoring Subteam Report (IGSDMS 2014) and are in Appendix 4. More refined data products are often available at regional to local scales. For example, Bureau of Land Management Rapid Ecoregional Assessments contain a large amount of geospatial data that may be useful in providing regional

information on vegetation types and persistent and land use and development threats across most of the range of sage-grouse (https://www.blm.gov/wo/st/en/prog/more/Landscape_Approach/reas.html). Also, high resolution geospatial data for cultivation risk layers are available and piñon and/or juniper landscape cover will soon be available for the eastern portion of the range (http://map.sagegrouseinitiative.com/). Land managers can evaluate the available land cover datasets for the targeted area and select those datasets with the highest resolution and accuracy.

Other Relevant Data Layers

Use of spatially explicit habitat models like those developed by Doherty et al. (2016) for GRSG is generally preferred over using threshold values for specific habitat variables like landscape cover of sagebrush (Cushman et al. 2013). However, in the absence of these models, individual habitat variables can provide important information on habitat characteristics and may provide a viable approach for assessing the probability of suitable habitat (Vojta et al. 2013). Landscape cover of sagebrush has been shown to be an important predictor of persistence of sage-grouse and other sagebrush obligate species and can help inform management decisions. Landscape cover of sagebrush is typically derived from remotely sensed land cover data such as LANDFIRE (USGS 2013) using a moving window analysis (see Appendix 5). Because of the difficulty of using remote sensing to assess landscape cover of sagebrush in the West-Central Semiarid Prairies (Management Zone I), landscape cover of sagebrush is less informative for this ecoregion than for the Wyoming Basin and Middle Rockies (Management Zone II) or for the Colorado Plateau and Southern Rockies (Management Zone VII). Areas containing sagebrush are commonly mapped as grassland types, because sagebrush is either an understory component or grass cover dominates the signature during the mapping process.

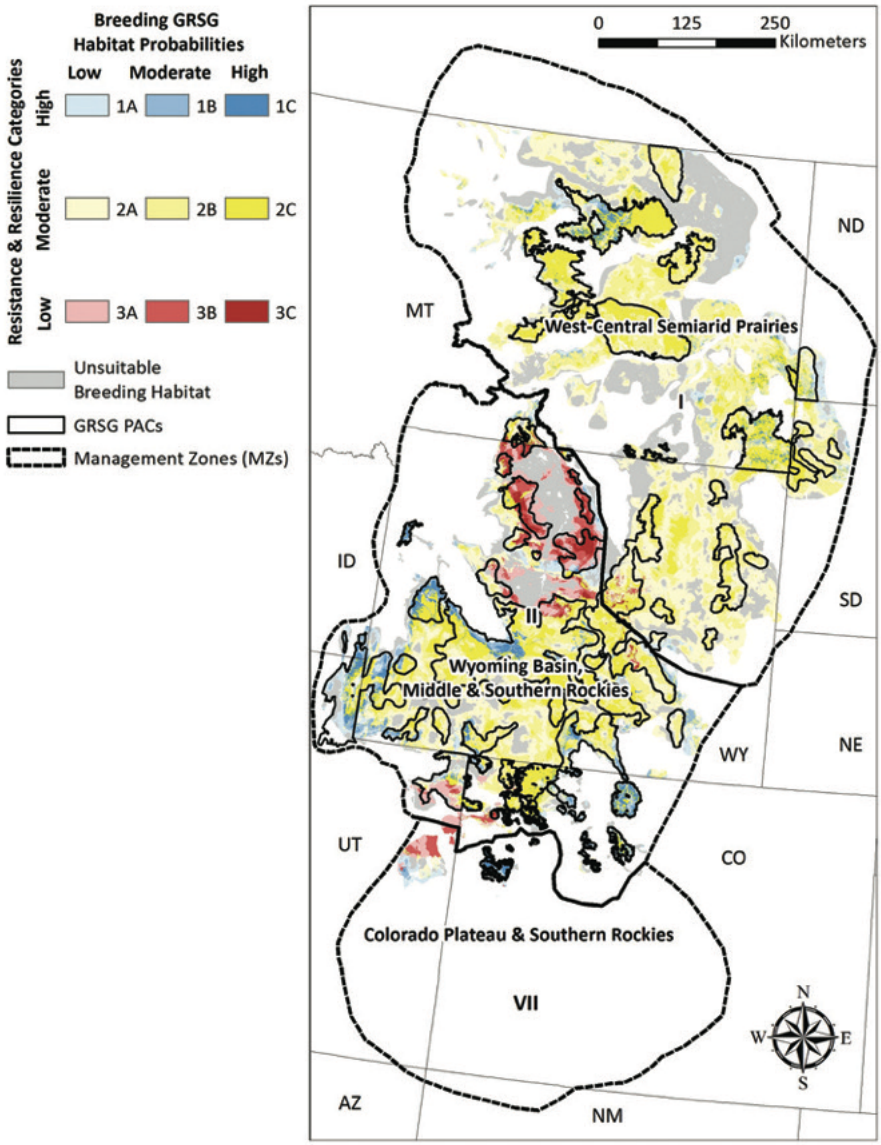
Analyses of the landscape cover of sagebrush around leks in various portions of the range (Aldridge et al. 2008; Knick et al. 2013; Wisdom et al. 2011) indicate that the relative probability of lek persistence can be estimated using percentage sagebrush landscape cover. In general, low lek persistence occurs with less than 25 percent landscape cover of sagebrush; intermediate persistence with 25–65 percent; and high persistence with more than 65 percent (see Chambers et al. 2014a for a detailed explanation). However, analyses conducted in Management Zone I for this report show that active leks are distributed across all of these sagebrush landscape cover categories (measured within 6.4 km of leks) indicating that GRSG select breeding habitat across a broader range of sagebrush landscape cover in Management Zone I than in other Management Zones. This finding reflects the relatively lower percentage of sagebrush landscape cover in Management Zone I (14 percent) than in Management Zone II (45 percent; Knick et al. 2011) where most active GRSG leks occurred in areas of high sagebrush cover. Similar relationships exist for other species in the region (Aldridge et al. 2011), and a recent rangewide analyses of sagebrush obligate passerine birds indicates that there is a threshold of about 40 percent landscape cover of sagebrush for predicted counts of several species (Brewer's sparrow [*Spizella breweri*], sagebrush sparrow [*Artemisiospiza nevadensis*], sage thrasher [*Oreoscoptes montanus*]) (fig. 27; Donnelly et al., in press).

Assessments of priority areas for management are typically conducted at the scale of ecoregions or Management Zones for GRSG because of similarities in biophysical characteristics and thus management strategies and treatments. Landscape scale analyses for GUSG are typically conducted at the scale of the range plus linkages. The process involves overlaying key data layers in a geospatial analysis to both visualize and quantify (1) species locations and abundances, (2) the probability that an area has suitable habitat, (3) the likely response to disturbance or management treatments, and (4) the dominant threats. The maps and analyses from this process are an essential component of prioritizing areas for management actions and developing management strategies.

The sage-grouse habitat resilience and resistance matrix (table 4) is based on the relative resilience and resistance of an area and the probability that the area provides suitable breeding habitat. The matrix provides the basis for interpreting the overlays and analyses and for selecting priority areas for management. Specific management strategies (table 5) address the predominant threats in sagebrush ecosystems and are linked directly to the cells in the matrix. These strategies are used to determine appropriate management actions for priority areas for management.

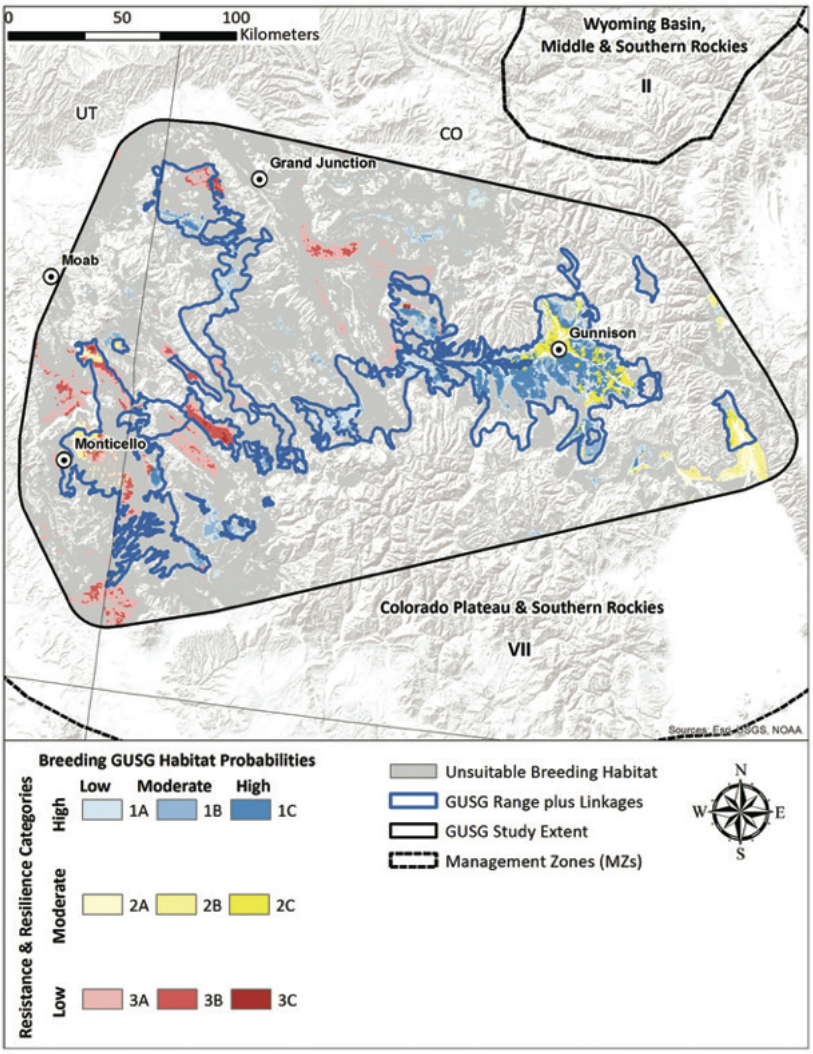
The steps in the geospatial analysis are identified below. The maps used to illustrate the steps are from the GRSG eastern range and the GUSG range and linkages.

1. Determine the best information available for the analyses. For GRSG, this includes Priority Areas for Conservation, breeding habitat probabilities, the population index (Doherty et al. 2016), and breeding bird densities (figs. 9, 23). For GUSG, this includes the range plus linkages, breeding habitat probabilities, and breeding bird densities (fig. 24).
2. Determine the probability of suitable habitat. For GRSG and GUSG, this is the breeding habitat probability (table 2; low = 0.25 to <0.50, moderate = 0.50 to <0.75, high = 0.75 to 1.0).
3. Create the resilience and resistance layer using categorized soil temperature and moisture regimes (figs. 7, 28, 29; Appendix 2; Maestas et al. 2016).
4. Overlay resilience and resistance categories with the probability of suitable habitat for the assessment area (figs. 30, 31). This layer provides information on how areas that can support sage-grouse will respond to both disturbance and management treatments, specifically the likelihood of recovery and risk of conversion to undesirable states. Calculating the areas in the different categories by ecoregion, Priority Areas for Conservation within Management Zones for GRSG, or the range plus linkages for GUSG can help identify priority areas for management.
5. Overlay resilience and resistance with species population abundance measures. For GRSG and GUSG, this is the breeding bird densities (figs. 32). This layer provides information on areas that currently support large populations, have potential to increase connectivity between populations, and are close enough to population centers that the species can recolonize reclaimed habitats. Calculating the areas in the different categories by ecoregion, Priority Areas for Conservation within Management Zones for GRSG, or the range plus linkages for GUSG can further refine areas for management.



aURHNj□—Greater sage-grouse breeding habitat probabilities based on 2010 to 2014 lek data (Doherty et al. 2016) intersected with resilience and resistance categories developed from soil temperature and moisture regimes in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.

6. Assess the extent and magnitude of the predominant threat(s). This will typically involve overlaying the resilience and resistance layer with the areas supporting high breeding habitat probabilities and the predominant threat(s). Threats vary by ecoregion/Management Zone for GRSG and within the range plus linkages for GUSG. Developing thresholds (ecological minimums) for the extent and magnitude of the threat (e.g., land cover of piñon and juniper and invasive annual grasses, density of oil and gas wells, road density, etc.) above which the habitat can no longer support sage-grouse and incorporating these into the geospatial analyses can further inform prioritization of areas for management. For example, ability of GRSG to maintain active leks decreases

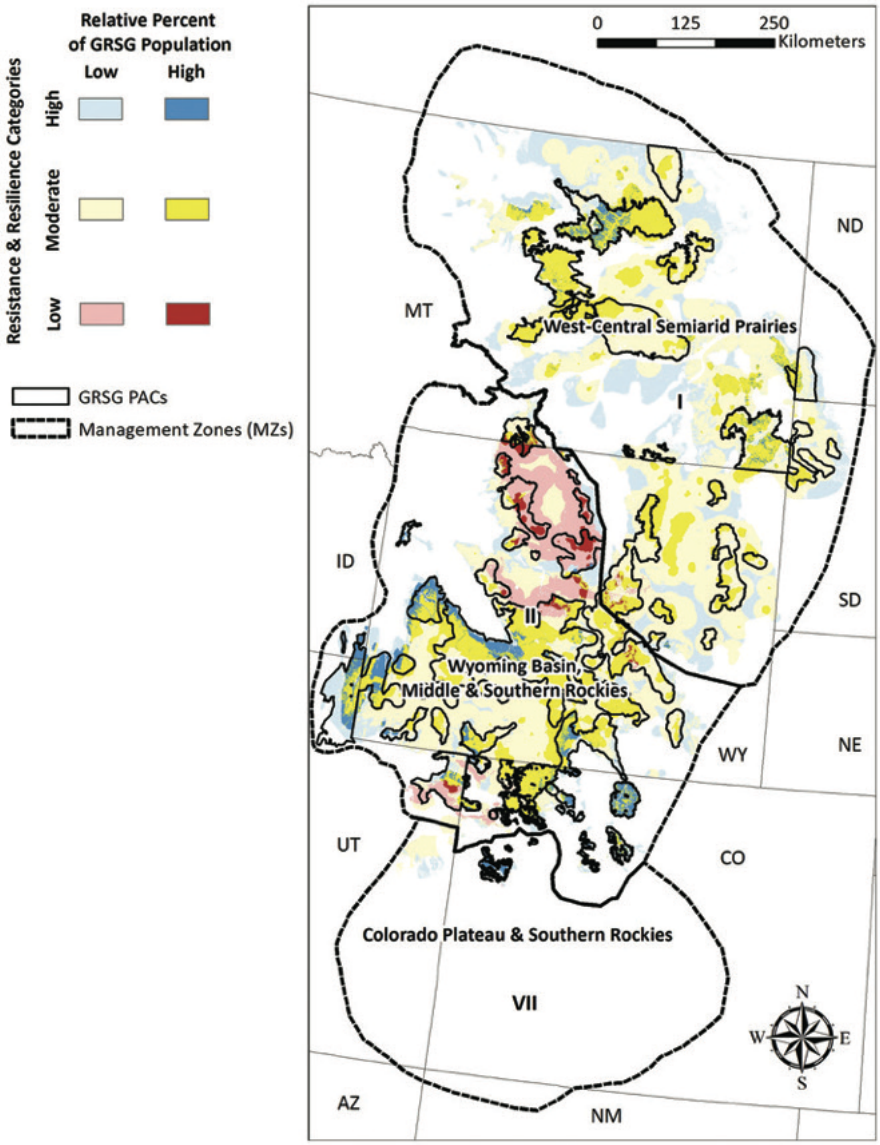


aURHNj□—Gunnison sage-grouse breeding habitat probabilities for the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) based on lek data from 1995 to 2015 intersected with resilience and resistance categories developed from soil temperature and moisture regimes. The breeding habitat probabilities were developed for this report based on Doherty et al. 2016. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.

significantly when conifer canopy exceeds 4 percent in the immediate vicinity (within 3,280 ft; 1000 m) of the lek (Baruch-Mordo et al. 2013), and most active leks average less than 1 percent conifer cover at landscape scales (3.1 mi; 5 km; Knick et al. 2013).

7. Prioritize areas for management. The maps and data derived from the prior steps and the sage-grouse habitat matrix (table 4) are used to determine priority areas for management within the assessment area. The actual prioritization is based on consideration of several factors:

   a. The area provides suitable habitat and supports species populations. For GRSG and GUSG, this is the breeding habitat probability and breeding bird density (table 4 cells 1B, 2B, 3B, 1C, 2C, 3C).



aURHNj —Relative percent of Greater sage-grouse population based on breeding abundance during 2010 to 2014 (Doherty et al. 2016) intersected with resilience and resistance categories developed from soil temperature and moisture regimes in Management Zones I, II, and VII (Stiver et al. 2006) and associated ecoregions (EPA 2016). The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3. A value of 80 percent is used to identify areas with high breeding abundance.

b. The area is at risk due to low resilience and resistance but has high conservation value for sage-grouse (table 4 cells 3B, 3C).
c. The area has reduced habitat suitability but could be improved by active management. These areas may be at higher risk of becoming unsuitable with additional disturbances that degrade habitat (table 4 cells 1B, 2B, 3B).

8. Determine the most appropriate management strategies. The maps and data derived from the prior steps and the sage-grouse habitat matrix (table 4) are also used to determine management strategies (table 5). At the scale of the ecoregion, or Priority Areas for Conservation within Management Zones for GRSG and range plus linkages for GUSG, management strategies

are developed that require interagency coordination, e.g., State, National Forest, etc. Examples of these types of strategies include: (1) prepositioning firefighting resources within fire-prone areas that provide suitable habitat and support species populations as is being done for areas in the Great Basin with high fire risk (USDI BLM 2014); (2) coordinating efforts to use early detection and rapid response to prevent expansion of invasive annual grasses and other weeds; and (3) assessing habitat connectivity among Priority Areas for Conservation and species populations to develop coordinated approaches to management strategies, such as conifer removal and other habitat improvements, to decrease fragmentation (e.g., Coates et al. 2016).

Differences in Resilience and Resistance, Breeding Habitat Probabilities, and Relative Percentage of the Population for the GRSG Management Zones

Here, a general overview of the similarities and differences in breeding habitat probabilities, relative percentage of population, and resilience and resistance is provided for Management Zones in the eastern portion of the range. Selecting priority areas for management will require more detailed analyses.

The area in GRSG Priority Areas for Conservation in Management Zones I and II is largest for moderate breeding habitat probabilities (46 percent and 43 percent), intermediate for high breeding habitat probabilities (33 percent and 31 percent), and smallest for low breeding habitat probabilities (19 percent and 21 percent), respectively (fig. 23; table 6). In Management Zone VII, the area in GRSG Priority Areas for Conservation is greatest for high breeding habitat probabilities (42 percent) followed by moderate (29 percent) and then low (24 percent). The area outside of Priority Areas for Conservation with high breeding habitat probability ranges from 8 percent in Management Zone VII, to 11 percent in Management Zone II, to17 percent in Management Zone I. This indicates significant acreages can be considered

zZO”j —The area and percentage of breeding habitat probability classes for Greater sage-grouse for Management Zones (MZ) I, II, and VII (A) and for priority area for conservation (PACs) within each Management Zone (B).

A

Breeding habitat probabilities	MZ I			MZ II			MZ VII		
	acres	km^2	%	acres	km^2	%	acres	km^2	%
High	5,488,682	22,212	12	6,586,037	26,653	18	114,492	463	10
Moderate	13,919,754	56,331	30	13,311,428	53,870	36	386,027	1,562	33
Low	15,693,021	63,507	34	11,330,253	45,852	31	532,736	2,156	45
Unsuitable	10,924,858	44,211	24	5,647,767	22,856	15	147,250	596	12
Total	46,026,314	186,262	100	36,875,485	149,230	100	1,180,506	4,777	100

B

Breeding habitat probabilities	MZ I PACs			MZ II PACs			MZ VII PACs		
	acres	km^2	%	acres	km^2	%	acres	km^2	%
High	3,914,390	15,841	33	5,285,823	21,391	31	96,865	392	42
Moderate	5,328,819	21,565	46	7,406,972	29,975	43	68,201	276	29
Low	2,170,323	8,783	19	3,564,243	14,424	21	55,599	225	24
Unsuitable	291,090	1,178	2	882,906	3,573	5	11,614	47	5
Total	11,704,623	47,367	100	17,139,944	69,363	100	232,279	940	100

for conservation and restoration actions both within the high habitat probability class in the Priority Areas for Conservation and in adjacent areas of high and especially moderate habitat probability.

The majority of the area within the GRSG Priority Areas for Conservation in each Management Zone is characterized by moderate resilience and resistance for Management Zone I and II (91 percent and 62 percent, respectively; fig. 28; table 7), and by high resilience and resistance for Management Zone VII (90 percent). A smaller percentage of habitat within Priority Areas for Conservation is in the low (1 percent) than high (8 percent) category in Management Zone I; similar percentages of habitat within Priority Areas for Conservation are in high (21 percent) and low (17 percent) in Management Zone II; and a small percentage of habitat within Priority Areas for Conservation is in either moderate (9 percent) or low (1 percent) in Management Zone VII. The large area within the high and moderate categories indicates that much of the eastern portion of the range within Priority Areas for Conservation has the capacity to recover from disturbances given appropriate management. However, areas in and adjacent to Priority Areas for Conservation, especially in Management Zone II, are characterized by low resilience and resistance. These areas are more susceptible to invasive annual grasses and require longer periods for recovery from either disturbances or management treatments (Chambers et al. 2014a; Mealor et al. 2012).

Coupling breeding habitat probabilities with resilience and resistance indicates that Priority Areas for Conservation generally have more area with high and moderate habitat probabilities and with moderate to high resilience and resistance than the Management Zones as a whole (fig. 30; tables 8, 9). In Management Zone I and II, most of the area within GRSG Priority Areas for Conservation is comprised of moderate to high breeding habitat probabilities with moderate resilience and resistance (fig. 30; table 9). In Management Zone VII, most of the area within the GRSG Priority Areas for Conservation is comprised of moderate to high breeding habitat probabilities with high resilience and resistance. Relatively small areas within the Priority Areas for Conservation have habitat probabilities that are unsuitable or low regardless of resilience and resistance class.

G5CE□□—The area and percentage of resilience and resistance classes for Management Zones (MZ) I, II, and VII (A) and for priority areas for conservation (PACs) within each Management Zone (B).

A

Resilience and probabilities	MZ I			MZ II			MZ VII		
	acres	km^2	%	acres	km^2	%	acres	km^2	%
High	21,993,546	89,005	28	25,270,281	102,265	43	17,614,769	71,285	47
Moderate	55,414,038	224,253	71	23,466,452	94,966	40	3,830,409	15,501	10
Low	145,724	590	1	9,913,884	40,120	17	16,297,510	65,954	43
Total	77,553,308	313,848	100	58,650,618	237,351	100	37,742,688	152,739	100

B

Resilience and probabilities	MZ I PACs			MZ II PACs			MZ VII PACs		
	acres	km^2	%	acres	km^2	%	acres	km^2	%
High	901,296	3,647	8	3,450,456	13,964	21	210,705	853	90
Moderate	10,549,022	42,690	91	10,384,371	42,024	62	20,400	83	9
Low	97,818	396	1	2,871,828	11,622	17	2,121	9	1
Total	11,548,135	46,734	100	16,706,656	67,610	100	233,226	944	100

G5CE□□—The area and percentage of breeding habitat probability class by resilience and resistance class for Greater sage-grouse for each Management Zone (MZ). Percentages within a Management Zone add to 100.

Breeding	Resilience and resistance								
lLB1L□	r/□			h/KDQLD□			a1wl□		
probability	acres	km^2	%	acres	km^2	%	acres	km^2	%
MZ I									
High	18,503	75	0	4,991,493	20,200	11	443,768	1,796	0
Moderate	69,366	281	0	12,986,234	52,554	29	720,665	2,916	2
Low	34,089	138	0	13,974,961	56,555	31	1,477,070	5,977	3
Unsuitable	12,319	50	0	7,503,099	30,364	17	3,241,274	13,117	7
Total	134,276	543	0	39,455,788	159,672		5,882,776	23,807	
MZ II									
High	796,172	3,222	2	4,586,273	18,560	13	1,121,366	4,538	3
Moderate	2,144,299	8,678	6	8,979,738	36,340	25	1,975,062	7,993	5
Low	2,313,881	9,364	6	6,325,700	25,599	18	2,411,600	9,759	7
Unsuitable	2,328,125	9,422	6	1,574,251	6,371	4	1,571,550	6,360	4
Total	7,582,478	30,685		21,465,962	86,870		7,079,578	28,650	
MZ VII									
High	1,530	6	0	4,277	17	0	108,532	326	9
Moderate	236,219	956	20	23,873	97	2	125,936	510	11
Low	173,717	703	15	102,109	413	9	256,693	1,039	22
Unsuitable	18,368	74	2	48,244	195	4	80,532	326	7
Total	429,833	1,739		178,503	722		571,693	2,200	

G5CE□□—The area and percentage of breeding habitat probability class by resilience and resistance class for Greater sage-grouse for priority areas for conservation (PACs) within each Management Zone (MZ). Percentages within a Management Zone add to 100.

Breeding	Resilience and resistance								
lLB1L□	r/□			h/KDQLD□			a1wl□		
probability	acres	km^2	%	acres	km^2	%	acres	km^2	%
MZ I PACs									
High	17,400	70	0	3,507,329	14194	30	359,745	1456	3
Moderate	59,363	240	1	4,882,662	19759	42	301,332	1219	3
Low	20,147	82	0	1,919,033	7766	17	192,156	778	2
Unsuitable	911	4	0	238,578	965	2	47,959	194	0
Total	97,822	396		10,547,602	42,685		901,192	3,647	
MZ II PACs									
High	673,119	2,724	4	3,547,203	14,355	21	993,466	4,020	6
Moderate	1,268,264	5,132	8	4,858,003	19,660	29	1,140,357	4,615	7
Low	799,051	3,234	5	1,734,161	7,018	10	881,707	3,568	5
Unsuitable	131,216	531	1	244,175	988	1	431,869	1,748	3
Total	2,871,650	11,621		10,383,542	42,021			13,951	
MZ VII PACs									
High	206	1	0	2,320	9	1	94,452	382	41
Moderate	1,591	6	1	3,512	14	2	63,245	256	27
Low	267	1	0	10,799	44	5	44,166	179	19
Unsuitable	25	0	0	3,384	14	1	8,156	33	4
Total	2,089	8		20,016	81		210,019	850	

Intersecting the resilience and resistance categories with the breeding bird densities provides information similar to the breeding habitat probabilities for GRSG Priority Areas for Conservation, but allows greater focus on areas known to support large populations of birds (fig. 32; tables 10, 11). A high percentage of the breeding bird density within both the Management Zones and Priority Areas for Conservation is within areas characterized by moderate resilience and resistance in Management Zones I and II, and by high resilience and resistance in Management Zone VII (tables 10, 11).

Examination of other data layers shows that different persistent ecosystem and land use and development threats exist across the eastern portion of the range and allows managers to focus on the primary threats to sage-grouse habitat within targeted areas. Cropland conversion is clearly one of the primary threats in the northern portion of Management Zone I (fig. 19). Oil and gas development is a threat across much of the eastern range, particularly the southern portion of Management Zone I, large areas of Management Zone II, and the northern and eastern portion of Management Zone VII (fig. 17).

Differences in Resilience and Resistance and Breeding Habitat Probabilities for the Gunnison Sage-grouse Range plus Linkages

Examining the breeding habitat probabilities and resilience and resistance for the GUSG the range plus linkages shows a high degree of diversity in habitat characteristics. Breeding habitat probabilities are classified as unsuitable (54 percent) or low (20 percent) for a relatively high percentage of the GUSG range plus linkages, while lesser amounts are classified as moderate (12 percent) or high (14 percent) (fig. 24; table 12). Areas with low resilience and resistance (34 percent) are generally found in the western portion of the range plus linkages, and areas with moderate (14 percent) to high (52 percent) resilience and resistance occur largely in the east and center portion of the range plus linkages (fig. 29; table 13). Intersecting the breeding habitat probabilities with resilience and resistance shows that areas with moderate to high breeding habitat probabilities are generally characterized by moderate resilience and resistance (fig. 31; table 14). This indicates that these areas likely have the potential to recover after disturbance and respond favorably to management actions.

zZO”j□ —Relative percentage of the Greater sage-grouse population by resilience and resistance class for Management Zones (MZ) I, II, and VII (A) and for priority areas for conservation (PACs) within each Management Zone (B).

A

Resilience and resistance	MZ I	MZ II	MZ VII
		Percent	
High	10	20	92
Moderate	90	70	6
Low	0	10	2

B

Resilience and resistance	MZ I PACs	MZ II PACs	MZ VII PACs
		Percent	
High	14	16	81
Moderate	55	54	2
Low	0	7	0

Table 11—Relative percentage of the Greater sage-grouse population with high and low breeding bird densities by resilience and resistance class for Management Zones (MZ) I, II, and VII (A) and for priority areas for conservation (PACs) within each Management Zone (B). High breeding bird density (High BBD) was defined as the smallest area that contained 80 percent of the breeding population of Greater sage-grouse within 26% to 34% of occupied breeding habitat within a Management Zone (see figure 11 in Doherty et al. 2016). Low breeding bird density (Low BBD) was defined as the area that contained all remaining breeding sage-grouse.

A

Breeding bird	**Resilience and resistance**		
KDN11NhG□	**r/□**	**h/KDQLD□**	**a1wl□**
	- - - - - - - - - - - - - - Percent - - - - - - - - - - - - - -		
MZ I			
High BBD	0	72	8
Low BBD	0	18	1
MZ II			
High BBD	6	57	17
Low BBD	4	13	3
MZ VII			
High BBD	2	3	76
Low BBD	1	2	16

B

Breeding bird	**Resilience and resistance**		
KDN11NhG□	**r/□**	**h/KDQLD□**	**a1wl□**
	- - - - - - - - - - - - - - Percent - - - - - - - - - - - - - -		
MZ I PACs			
High BBD	0	49	7
Low BBD	0	6	7
MZ II PACs			
High BBD	0	48	15
Low BBD	0	6	1
MZ VII PACs			
High BBD	0	1	68
Low BBD	0	1	13

Table 12—The area and percentage of Gunnison sage-grouse breeding habitat probability classes in the Gunnison sage-grouse rnage plus linkages.

dE5ww□	t,4w□	t45yH ^{2}□	**Percent**
High	261,317	1,058	12
Moderate	303,683	1,229	13
Low	400,177	1,619	18
Unsuitable	1,273,925	5,155	57
Total	2,239,102	9,061	100

Table 13—The area and percentage of resilience and resistance classes in the Gunnison sage-grouse range plus linkages.

dE5ww□	t,4.w□	t4.5yH	²□	Percent
High	1,268,414	5,133		52
Moderate	339,267	1,373		14
Low	831,168	3,364		34
Total	2,438,849	9,870		100

G5CE.□ —The area and percentage of breeding habitat probability class by resilience and resistance class for the Gunnison sage-grouse range plus linkages. Percentages add to 100.

	Resilience and resistance								
yQDDK1NwlLB1L□	r/□			h/KDQLD□			a1wl□		
ZQ/BLB1V1□	kvQD□	kQDL3z	²□ □	kvQD□	kQDL3z	²□ □	kvQD□	kQDL3z	²□ %
High	5,067	21	1	69,622	282	3	175,097	708	8
Moderate	64,865	262	3	60,723	246	3	163,007	659	7
Low	118,930	481	5	43,721	177	2	232,846	942	11
Unsuitable	547,486	2,216	25	161,010	652	7	561,051	2,270	25
Total	736,348	2,980		335,076	1,357		1,132,001	4,579	

□1.4HLWLWBtOO4PO4L5l.f5W5B.H.WlG4.5lH.Wlw5l□
Local Scales

Once priority areas and overarching strategies are identified, higher resolution spatial data are combined with local information and knowledge to determine the most appropriate management strategies and identify project areas. The sage-grouse habitat matrix and the general criteria for prioritizing areas for management in Step 7 of the prior section can aid in selecting areas for treatment that will benefit sagebrush ecosystems and species populations. Also, information on the resilience and resistance of the area and the predominant threats can help in determining appropriate management strategies and treatments (table 5).

6j5PU.V6SjcN4EjPP

Steps in the process of determining the suitability of an area for treatment and the most appropriate treatment(s) include: (1) identify the different ecological sites that occur across the area and determine their relative resilience to disturbance and resistance to invasive annual grasses; (2) evaluate the current ecological dynamics of the ecological sites and, where possible, their restoration pathways; and (3) select actions with the potential to increase ecosystem functioning and habitat connectivity (see Miller et al. 2014, 2015; and Pyke et al. 2015a,b for detailed descriptions of this process). Anticipating changes like climate warming and monitoring management outcomes can be used to adapt management practices over time. A general approach using questions to identify the information required in each step is shown in table 15. These questions can be modified to include the specific information needed for each project area and for treating different ecological sites.

zZO”j□ —Questions and considerations for conducting fuels management, fire rehabilitation, and restoration treatments (modified from Miller et al. 2014, 2015).

Steps in the process	Questions and considerations
I. Assess potential treatment area and identify ecological sites	Rk 4 54 O4LP4LIZ54 5w P4 (EwH5W5B H WI4 4k5CLEL I5ILPWP44w toration within the focal area? Consider sage-grouse habitat needs and resilience and resistance. 2. What are the topographic characteristics and soils of the area? Verify soils mapped to the location and determine soil temperature/moisture regimes. Collect information on soil texture, depth and basic chemistry for restoration projects. 3. How will topographic characteristics and soils affect vegetation recovery, plant establishment and erosion? Evaluate erosion risk based on topography and soil characteristics. 4. What are the potential native plant communities for the area? Match soil components to their correlated ESDs. This provides a list of potential species for the site(s).
II. Determine current state of the site	5. Is the area still within the reference state for the ecological site(s)?
III. Select appropriate action	6. How far do sites deviate from the reference state? How will treatment success be measured? Pw(L WIO 4 WWL5Ewk4(Cw5WJO 4 WWL5EB45ww w5WJ R4w zLwIIP facilitate recovery? 8. Are invasive species a minor component? 9. Do invasive species dominate the sites while native life forms are missing or severely under represented? If so, active restoration is required to restore habitat. 10. Are species from drier or warmer ecological sites present? Restoration with species from the drier or warmer sites should be considered. 11. Have soils or other aspects of the physical environment been altered? Sites may have crossed a threshold and represent a new ecological site IZO 4 (L4LWBW xwLI wO L l4 5IH WI4 wIP45ILPW5OO4P5 kw
IV. Determine posttreatment management	12. How long should the sites be protected before land uses begin? In general, sites with lower resilience and resistance should be protected for longer periods. 13. How will monitoring be performed? Treatment effectiveness monitoring includes a complete set of measurements, analyses, and a report. 14. Are adjustments to the approach needed? Adaptive management is 5OOEL JIP (I(4 O4PK IwC5w JPW PWwLwI WIW JLWBw 4PHHI(E locations.

Ecological Site Descriptions

Ecological site descriptions (ESDs) and their associated state-and-transition models provide essential information for determining treatment feasibility and type of treatment. Ecological site descriptions are part of a land classification system that describes the potential of a set of climate, topographic, and soil characteristics and natural disturbances to support a dynamic set of plant communities (Bestelmeyer et al. 2009; Stringham et al. 2003). Soil survey data from the Natural Resource Conservation Service (http://soils.usda.gov/survey/), including soil temperature/moisture regimes and other soil characteristics, are integral to the development of ecological site descriptions. The Natural Resource Conservation service and their partners have developed ecological site descriptions to assist land management

agencies and private landowners with making resource decisions and are often available for the sage-grouse Management Zones. For a detailed description of ESDs and access to available ESDs see: http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/.

Ecological site descriptions assist managers to step-down generalized vegetation dynamics, including the concepts of resilience and resistance, to local scales. For example, variability in soil characteristics and the local environment (e.g., average annual precipitation as indicated by soil moisture regime) can strongly influence both plant community resilience to disturbance as well as the resistance of a plant community to nonnative invasive species (tables 3, 4). Within a particular ecological site description, there is a similar level of resilience to disturbance and resistance to nonnative invasive species. This information can be used to determine the most appropriate management actions.

A tool has recently been developed through the Web Soil Survey that produces a Resilience and Resistance Score Sheet Soils Report for the Great Basin based on the approach developed in Miller et al. (2014, 2015) (http://websoilsurvey.nrcs.usda.gov/app/). This tool provides managers with necessary information to assess the soils characteristics of a project area and determine its relative resilience to disturbance and management treatments and resistance to nonnative invasive annual grasses. It can be adapted to the eastern range.

State-and-Transition Models

These models are a central component of ecological site descriptions and are widely used by managers to illustrate changes in plant communities and associated soil properties, causes of change, and effects of management interventions (Briske et al. 2005; Stringham et al. 2003; USDA NRCS 2015a). State-and-transition models have been developed for sagebrush ecosystems (Barbour et al. 2007; Boyd and Svejcar 2009; Chambers et al. 2014c; Forbis et al. 2006; Holmes and Miller 2010). These models describe the alternative states, ranges of variability within states, and processes that cause plant community shifts within states as well as transitions among states within ecological types or sites (Caudle et al. 2013).

State-and-transition models use the concepts of ***states*** (a relatively stable set of plant communities that are resilient to disturbance) and ***transitions*** (change among alternative states caused by disturbances or drivers) to describe the range in composition and function of plant communities within ecological site descriptions (Stringham et al. 2003; see Appendix 1 for definitions). The reference state is based on the natural range of conditions associated with natural disturbance regimes and often includes several plant communities (***phases***) that differ in dominant plant species relative to type and time since disturbance (Caudle et al. 2013). Alternative states describe new sets of communities that result from factors such as inappropriate livestock use, invasion by nonnative species, or changes in fire regimes. Changes or transitions among states often are characterized by ***thresholds*** or conditions that may persist over time without active intervention, potentially causing irreversible changes in community composition, structure, and function. ***Restoration pathways*** are used to identify the environmental conditions and management actions required for return to a previous state.

Generalized state-and-transition models that follow current interagency guidelines (Caudle et al. 2013) and that are aligned with the dominant ecological types in table 3 are provided in Appendix 6. These state-and-transition models are

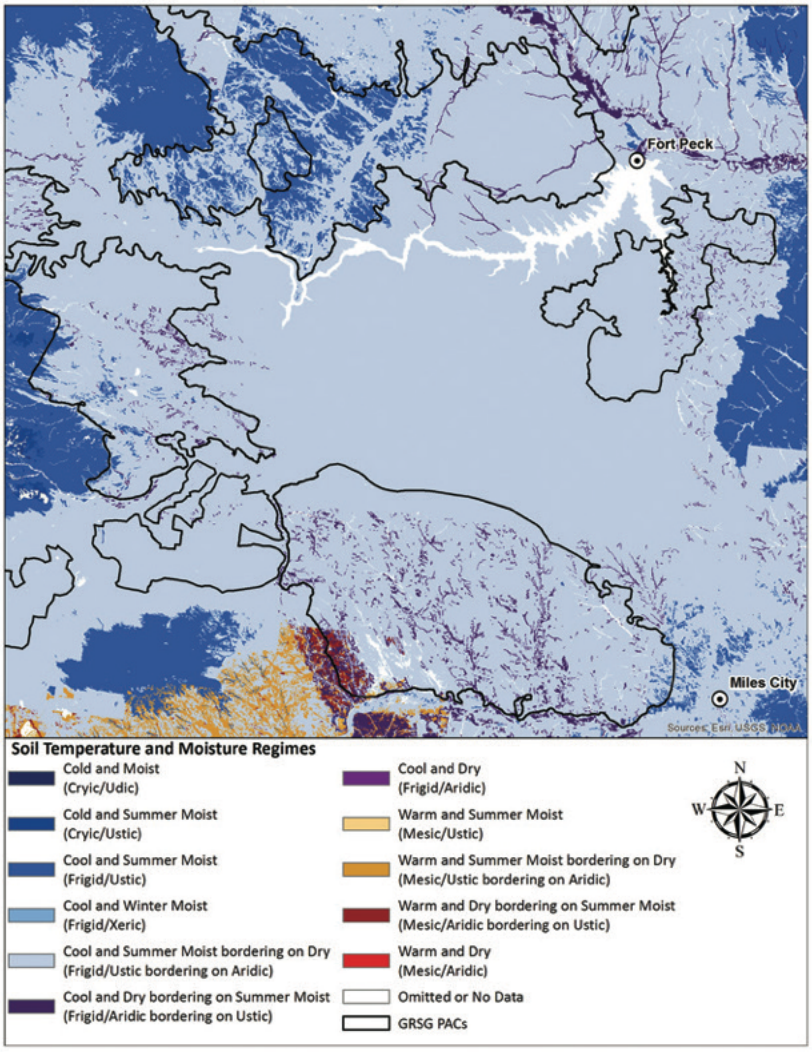
generally applicable to Management Zone I (West-Central Semiarid Prairies) and Management Zones II and VII (Wyoming Basin and Central Middle Rockies, and Colorado Plateau and Southern Rockies).

m/ZC5"jP4Gu4764e55"86Sjr4VEj56PZVxz44"P

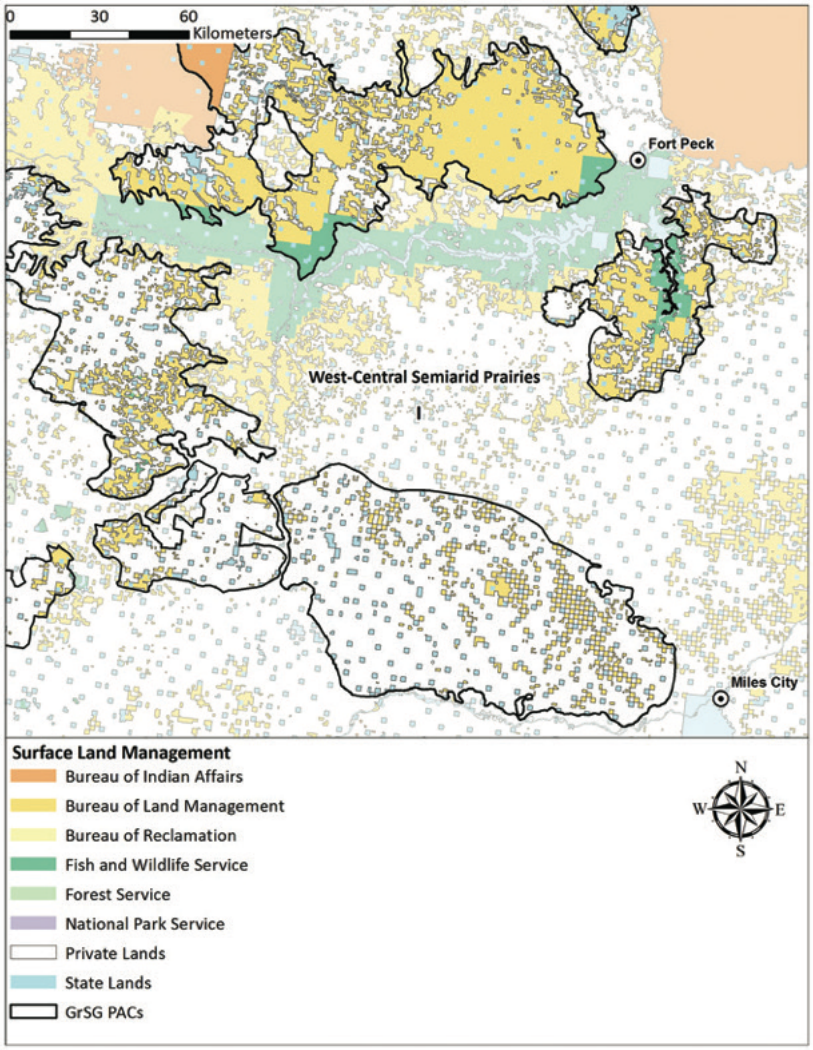
Examples of the approach discussed in this report are provided below for two areas that support GRSG populations and one area that supports GUSG populations. These areas differ in relative resilience and resistance as indicated by soil temperature and moisture regimes and the dominant habitat threat.

Example #1: East-central Montana

This area is characterized primarily by cool and summer moist bordering on dry soil temperature and moisture regimes (fig. 33) with moderate resilience and resistance (table 4 cells 2A, 2B, 2C). Most of the area is privately owned (fig. 34),



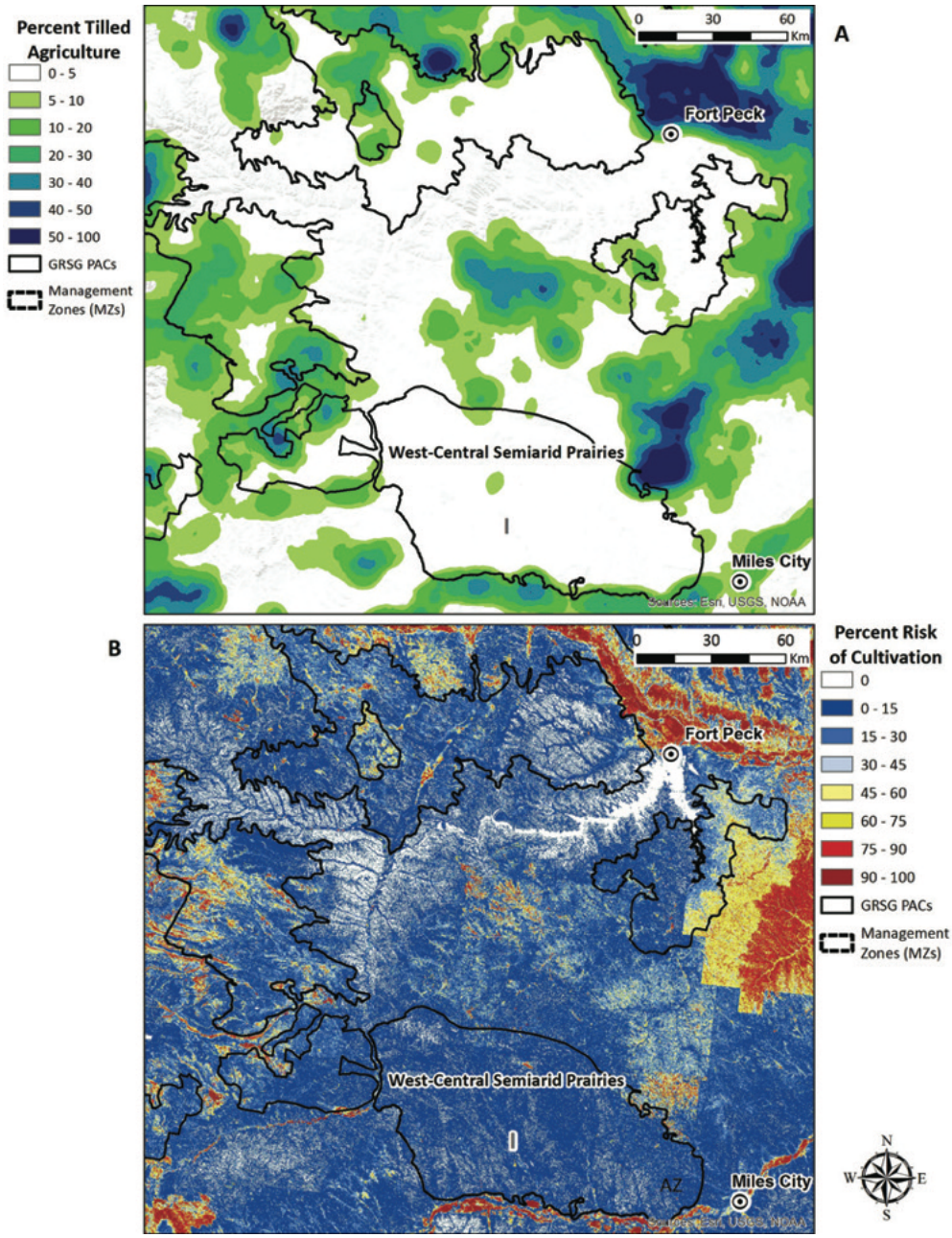
āURHNj□—Soil temperature and moisture regimes by soil moisture subclass for an area in eastern Montana. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.



āURHNj□—Surface land management for an area with agricultural conversion in eastern Montana (BLM 2015).

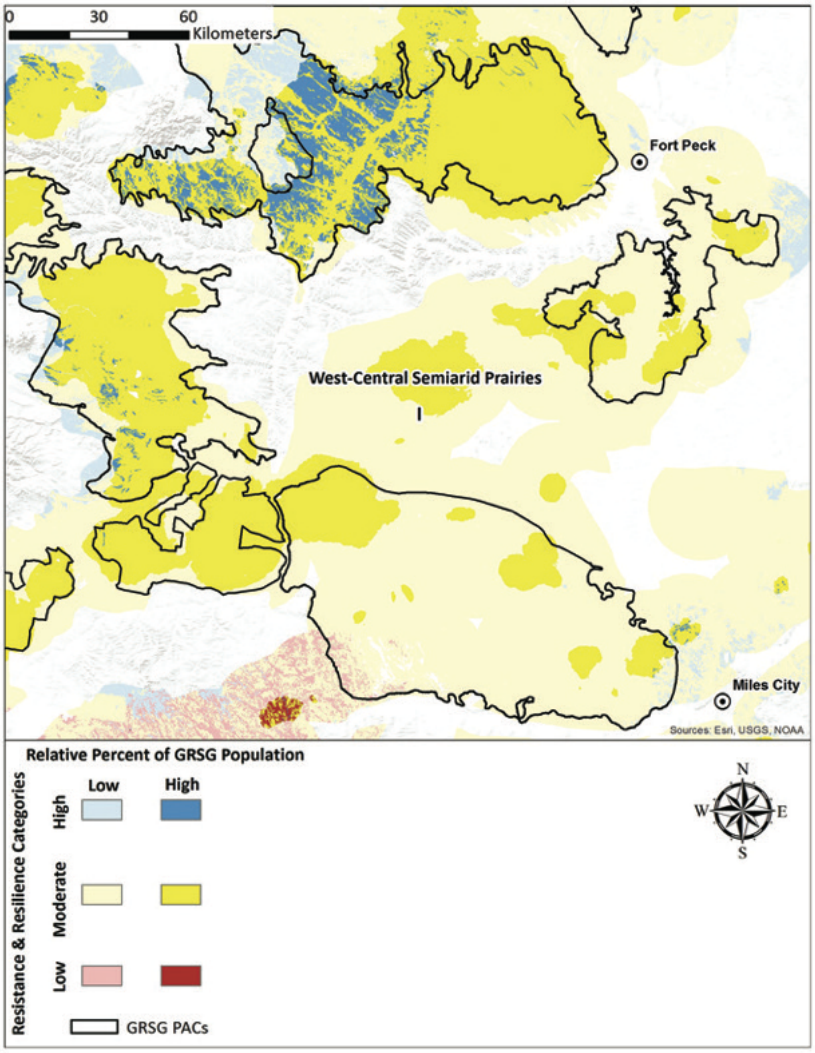
and large cropland areas exist adjacent to Priority Areas for Conservation with moderate to high GRSG populations (fig. 35a, 36). Areas on private lands that support high breeding habitat probabilities and that have or are adjacent to high population concentration centers could be targeted for conservation easements, term easements, or other conservation options to keep native rangelands intact. Also, USDA and state-based initiatives may provide incentives for transitioning expiring Conservation Reserve Program (CRP) or other cultivated lands to rangelands that support perennial plant communities. The Sage-Grouse Initiative (SGI) Cultivation Risk layer (Smith et al. 2016; http://map.sagegrouseinitiative.com/) along with existing cropland cover maps can be used to help identify areas that have not yet been plowed but may be at high risk of future conversion due to suitable climate, soils, and topography (fig. 35b; Smith et al. 2016).

A generalized state-and-transition model for the dominant ecological type in this area identifies the alternative states and transitions for this type (fig. A6.3). Following prolonged drought, improper grazing, and frequent sagebrush control treatments, the site can transition to an alternative state that is dominated by low



—(A) Percent annually tilled agricultural land (NASS 2014) within 5.0 km of each pixel for an area in eastern Montana. (B) Percent risk of cultivation for the same area derived from the Sage-Grouse Initiative cultivation risk mapping tool (http://map.sagegrouseinitiative.com/), which is based on climate, soils, and topography.

statured cool season and sod-forming grasses (fig. A6.3). In the absence of fire and sagebrush control treatments, the site can transition to heavy sagebrush dominance with few grasses and forbs. These altered states are susceptible to a variety of non-native invasive plants such as Russian Knapweed (*Cenaurea repens*), field brome, and cheatgrass (see http://invader.dbs.umt.edu/queryarea.asp for a complete county list), and early detection and rapid response can be used in all areas with high to moderate habitat probabilities and breeding bird concentrations to limit establishment of these invasive species (see table 5). Livestock management that maintains



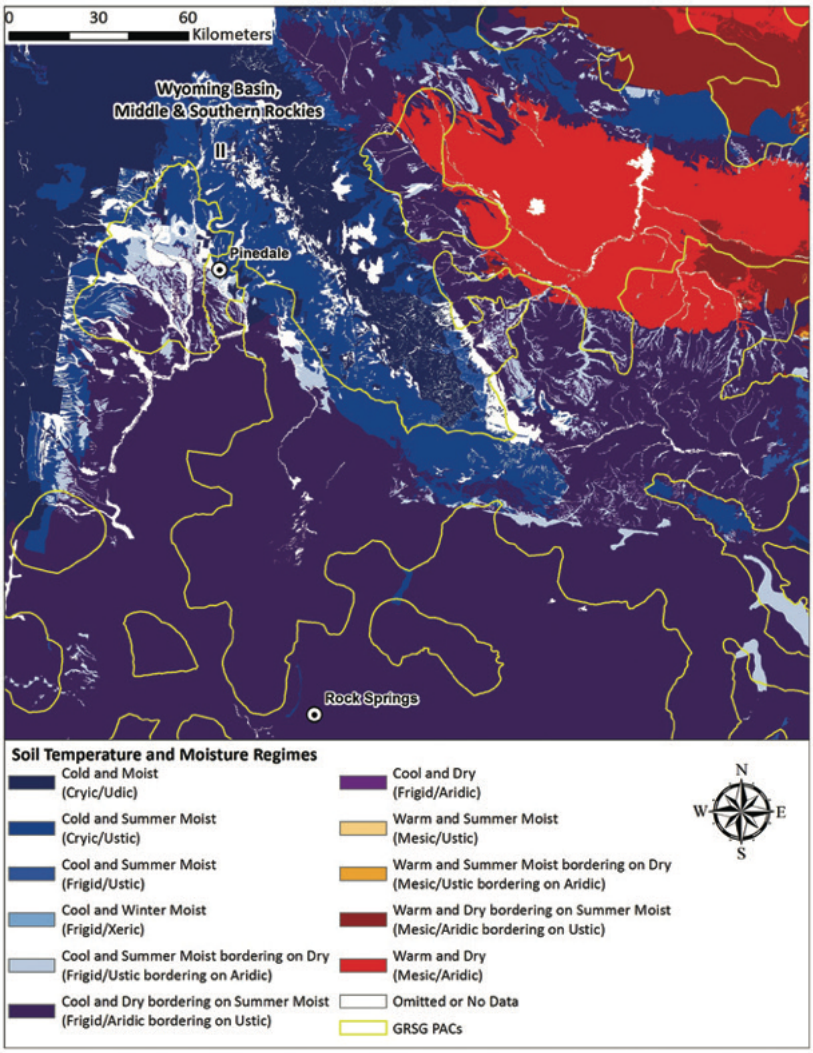
aURHNj—Relative percent of Greater sage-grouse population based on breeding abundance during 2010 to 2014 (Doherty et al. 2016) intersected with resilience and resistance categories developed from soil temperature and moisture regimes for an area in eastern Montana. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3. A threshold value of 80 percent is used to identify high breeding concentration centers.

a balance of native perennial grasses (cool and warm season species) and forbs will allow natural regeneration of sagebrush and increase competitive ability with nonnative invasive plants. Also, an altered/seeded state exists where introduced perennial grasses such as crested wheatgrass were seeded onto former croplands. These introduced perennial grasses can prevent establishment of sagebrush and other native species and spread into and dominate sagebrush ecosystems (Lessica and Deluca 1996). Thus further seeding of these species following disturbances is not recommended.

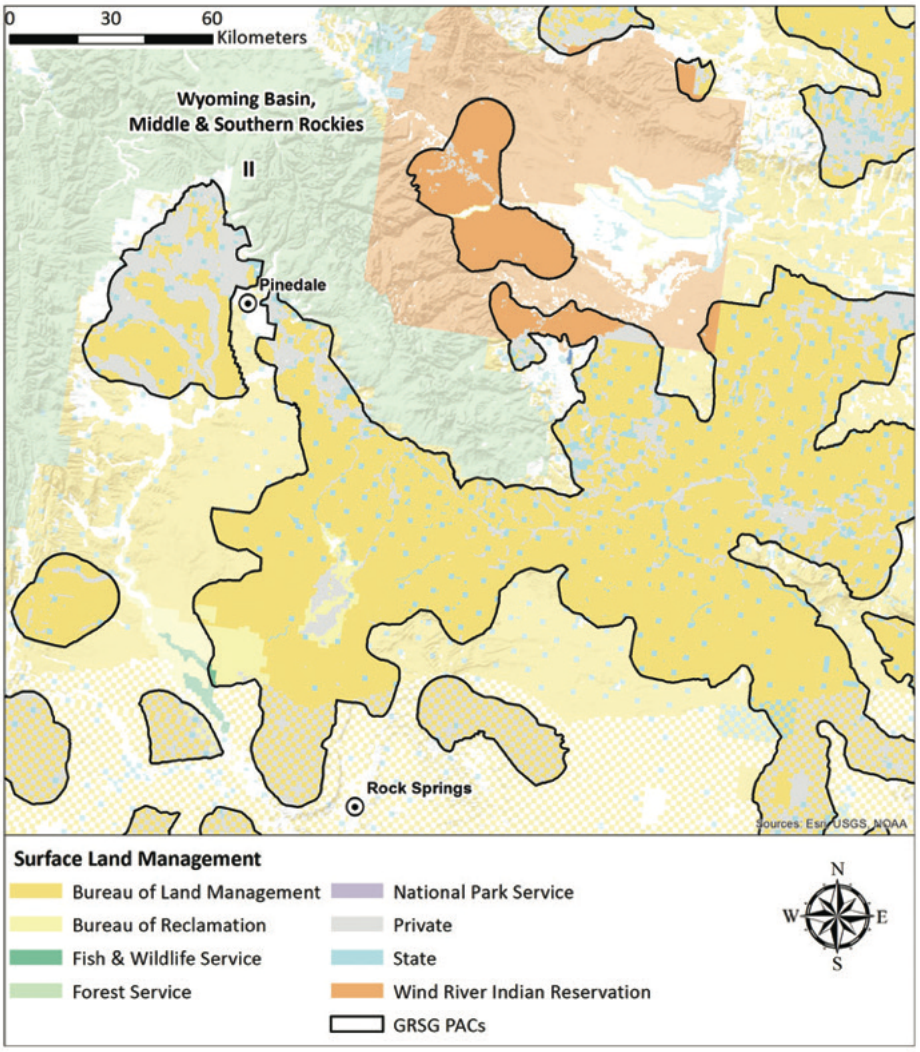
Example #2: Southwestern Wyoming

This area is characterized by mountainous terrain with sagebrush ecosystems that range from cold and summer moist to warm and dry bordering on summer moist and thus have high to low resilience and resistance (fig. 37). Surface land management is primarily USFS, BLM, and private (fig. 38). The area has wide-spread oil and gas development along with high GRSG concentration areas (figs. 39, 40).

In areas with high habitat probabilities and breeding concentration centers avoiding development and fragmentation where feasible and consistent with existing State and Federal conservation plans is recommended regardless of resilience and resistance category (table 4 cells 1C, 2C, 3C). Reducing energy and other transport corridors as well as vehicle access where consistent with the above mentioned plans can also minimize fragmentation. Exurban residential development is also fragmenting habitats and conservation easements can be an important tool for ameliorating this threat (fig. 41).

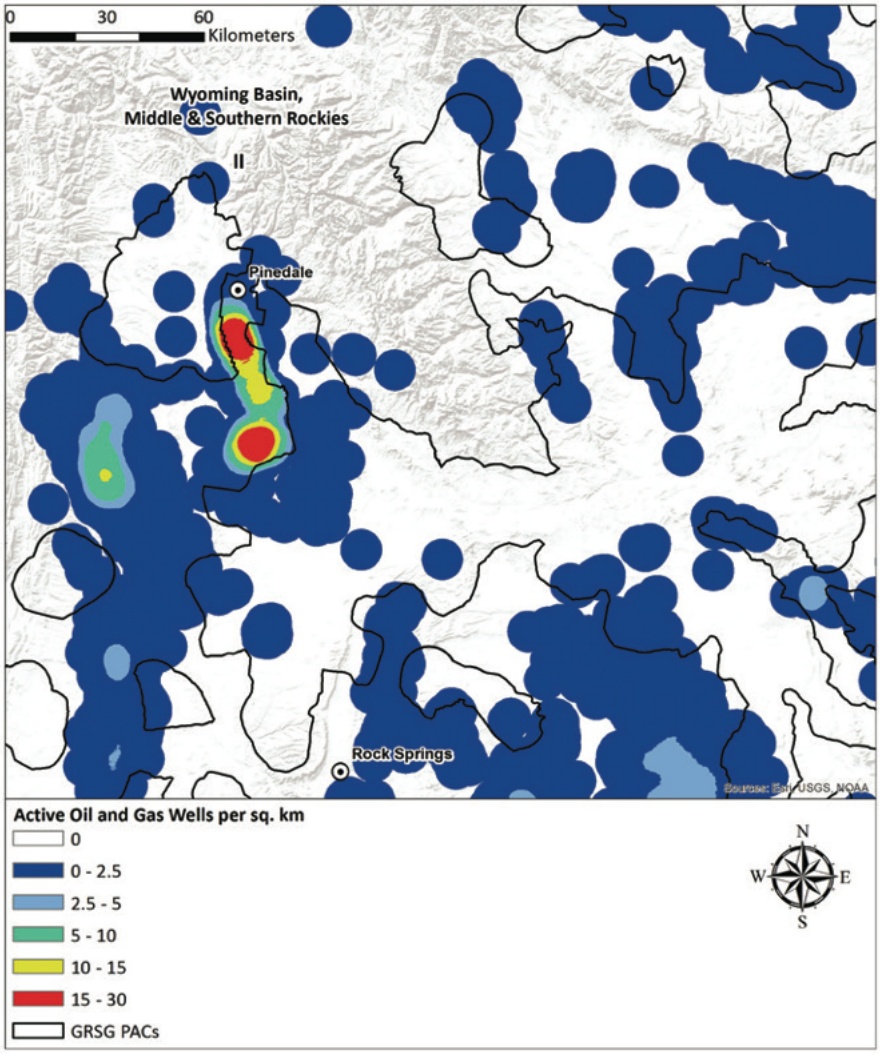


āURĦNj□—Soil temperature and moisture regimes by soil moisture subclass for an area in southwest Wyoming with oil and gas development. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.



aURHNj —Surface land management for an area with oil and gas development in southwest Wyoming (BLM 2015).

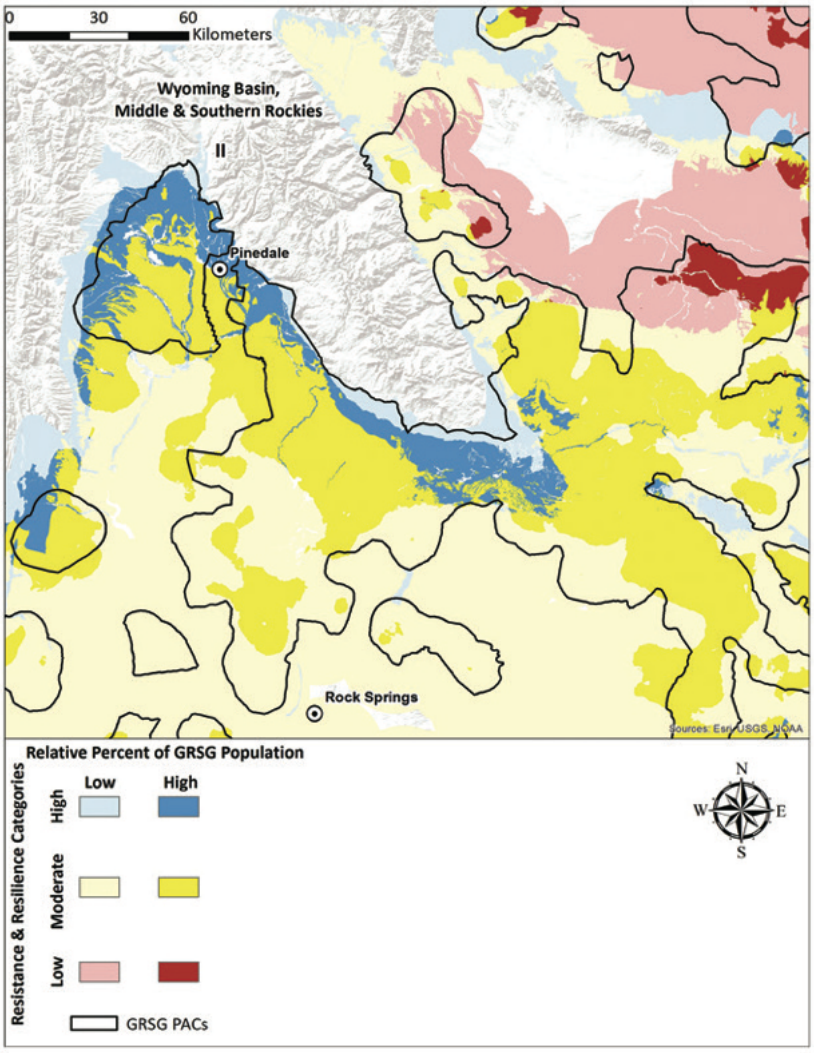
Because of the wide range of soil temperature and moisture regimes, the area supports several ecological types. Relevant state-and-transition models for these types are in Appendix A (figs. A.6.5, A.6.6, A.6.7, A.6.9, A.6.10). In general, continuous, heavy grazing of cool season grasses during the critical growth period can result in an alternative state dominated by grazing tolerant species. Further grazing can result in an eroded state that is highly susceptible to nonnative invasive species. Fire is rare, but multiple chemical or mechanical treatments or biological disturbances that reduce sagebrush can result in a sprouting shrub state. For these states, livestock grazing strategies can be designed to improve the condition of native plant communities and decrease nonnative invasive plant species. Strategies that include periodic rest during the critical growth period, especially for cool season grasses, can increase native species and minimize invasion. This strategy is particularly important in areas with low resilience and resistance. Given climate warming, management aimed at restoring understory grasses and forbs has the potential to increase resilience and resistance to both drought and fire.



aLB(4 —Number of active oil and gas wells per square kilometer (IHS; BLM [AFMSS]) for an area in southwest Wyoming.

The area is susceptible to numerous nonnative invasive plants and proactive weed management is recommended in all areas with high habitat suitability and breeding concentration centers (see table 5). Nonnative invasives include several *Bromus* species such as cheatgrass and field brome, *Poa* species such as bulbous bluegrass (*P. bulbosa*) and Kentucky bluegrass (*P. pratense*), spotted and Russian knapweed, diffuse knapweed (*Centauria diffusa*), Canada thistle (*Cirsium arvense*), and bull thistle (*Cirsium vulgare*) among others (http://invader.dbs.umt.edu/queryarea.asp). Preventing the spread of large weed infestations from areas with lower habitat probabilities can protect higher quality habitat.

For disturbances that remove vegetation and cause soil disturbance such as well pads and roads, impacts can be minimized through best management practices identified in State and Federal conservation plans, such as top soil banking, using certified weed-free (including annual bromes) seed mixes, appropriate seeding



aLB(4 —Relative percent of Greater sage-grouse population based on breeding abundance during 2010 to 2014 (Doherty et al. 2016) intersected with resilience and resistance categories developed from soil temperature and moisture regimes for an area in southwest Wyoming. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3. A threshold value of 80 percent is used to identify high breeding concentration centers.

technologies, and monitoring. In low resilience and resistance areas, multiple interventions may be required to restore sagebrush habitat. Numerous introduced plant species including crested wheatgrass and several *Medicago* species, such as alfalfa and *Trifolium* species (clovers), occur in this area. Seeding these species for reclamation or restoration of sagebrush habitat can be avoided, especially in cooler and moister areas where native species establish well.

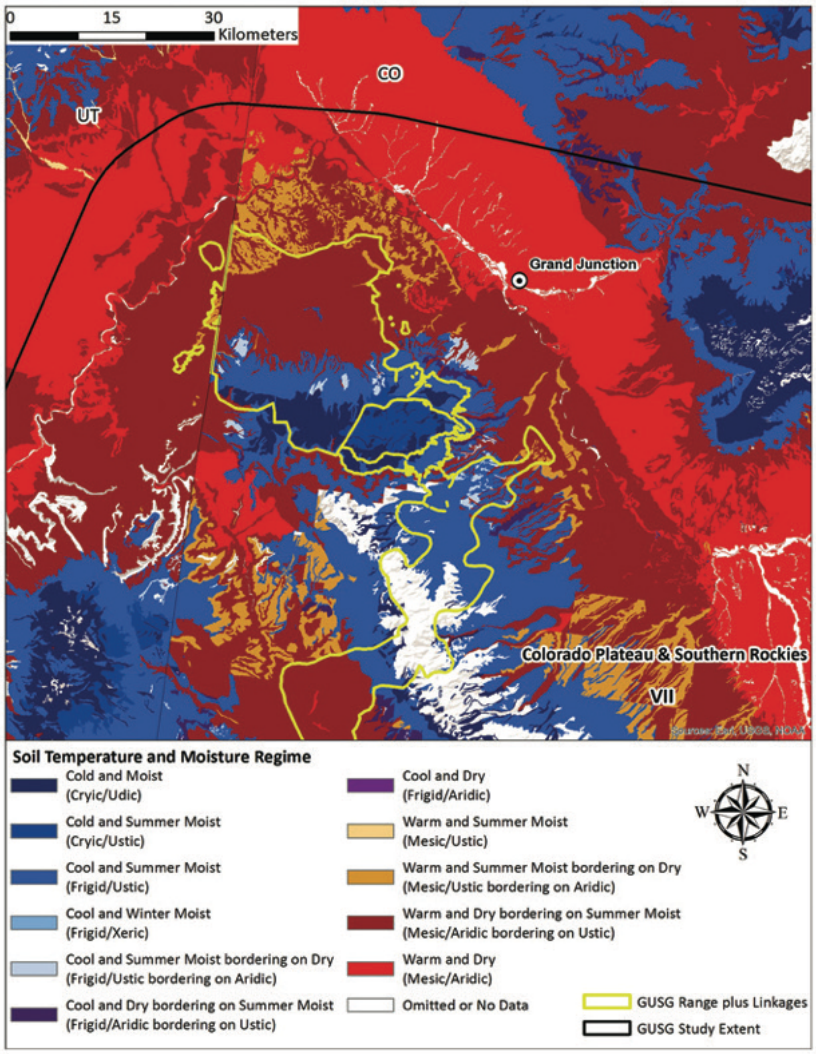


aLB(4 —A conservation easement near Pinedale, Wyoming (photo by Jeremy Roberts, Conservation Media; used with permission).

Example #3: Piñon Mesa Population of Gunnison Sage-Grouse in Central Colorado

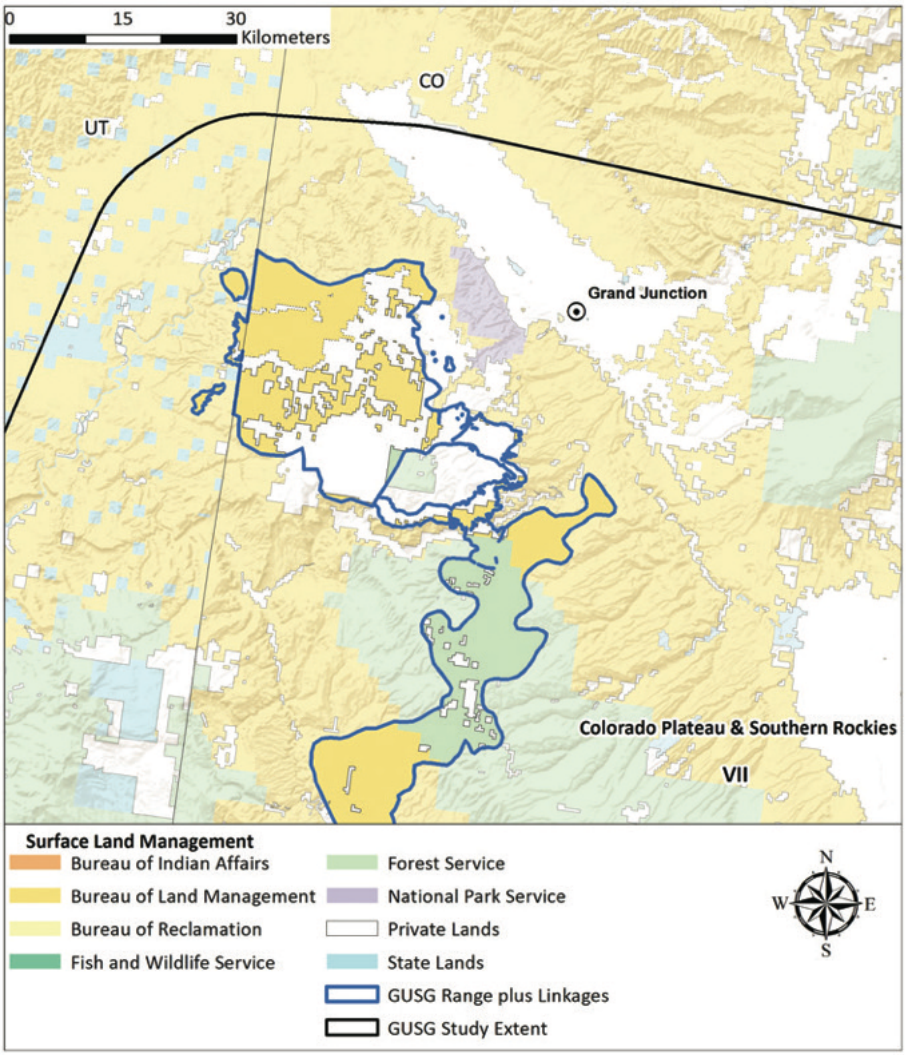
This area is characterized by mountainous terrain with sagebrush ecosystems that range from cold and moist to warm and dry bordering on summer moist (fig. 42). Surface land management is primarily Bureau of Land Management, U.S. Forest Service, and private (fig. 43). This area has high GUSG breeding habitat probabilities with relatively large breeding concentration centers and is threatened by conifer expansion, primarily two-needle piñon and Utah juniper (figs. 44, 45).

A state-and-transition model for a dominant ecological type on the *Piñon Mesa* identifies the alternative states and transitions for the type (fig. A6.8). In general, improper livestock use, such as heavy grazing during the critical growth period, can decrease perennial grasses and forbs, increase woody biomass (fuel loads), and elevate susceptibility to invasive annual grasses. Research on the Uncompahgre Plateau indicates that old growth piñon and juniper stands are common and range from relatively open and juniper dominated at low elevations to closed canopied and piñon dominated at higher elevations (Shinneman and Baker 2009). Improper livestock grazing after Euro-American settlement in the late 1800s likely reduced understory grasses and forbs (Shinneman and Baker 2009). This, in turn, decreased competition with tree seedlings and facilitated tree establishment, primarily two-needle piñon, during favorable climatic periods (Shinneman and Baker 2009). Tree infilling is occurring locally and fires in piñon and juniper stands at or near full tree stocking are typically of high severity (Baker and Shinneman 2004).



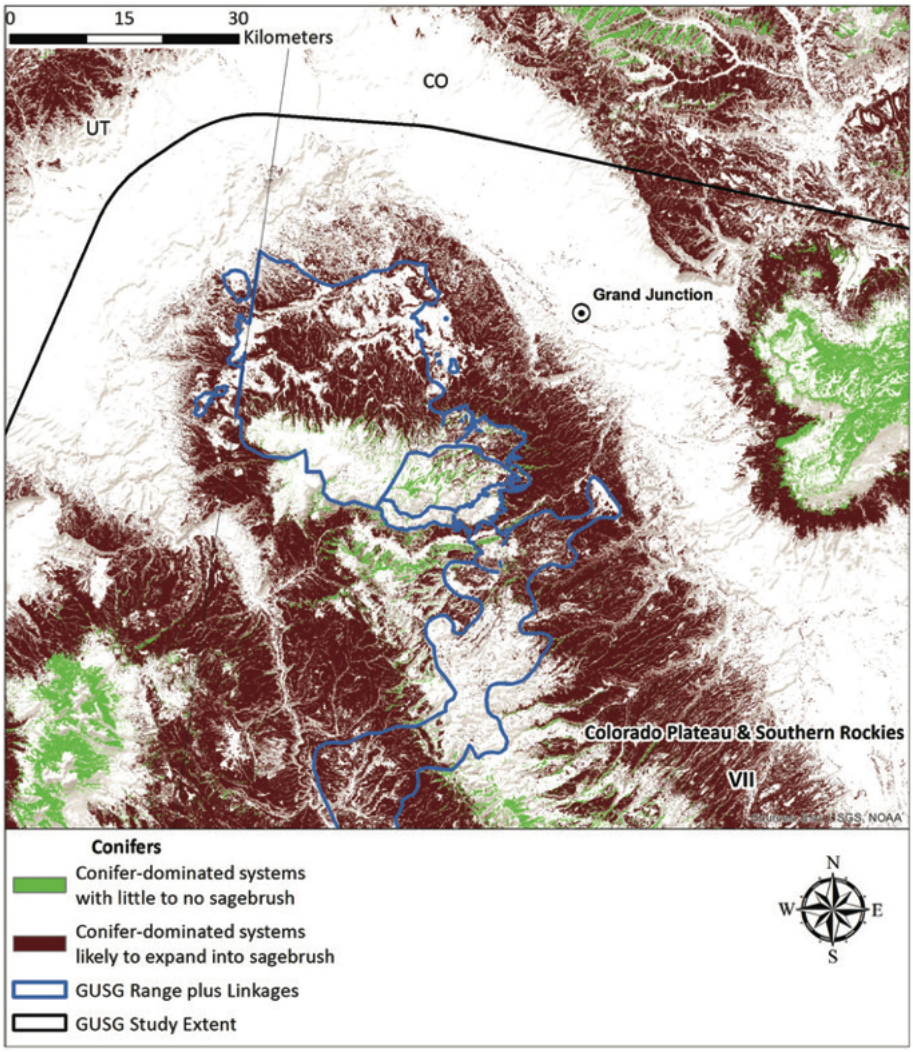
aLB(4 —The soil temperature and moisture regimes by soil moisture subclass for an area in the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) with piñon and juniper expansion (Mesa County, Colorado). The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.

Infilling of trees and/or improper livestock grazing can result in reductions in understory sagebrush and cool season grasses and increase susceptibility to invasion by cheatgrass. In southwestern Colorado in Mesa Verde National Park, piñon and juniper stands that had sparse understories prior to burning are now dominated largely by cheatgrass and other annual invaders (Floyd et al. 2006). Increases in invasive annual grasses may cause more frequent and continuous fires and result in conversion to alternative states dominated by annuals (Floyd et al. 2006). Proper management of livestock grazing can promote native perennial grass and forb growth and reproduction and maintain or enhance resilience to wildfires and resistance to invasive annual grasses.



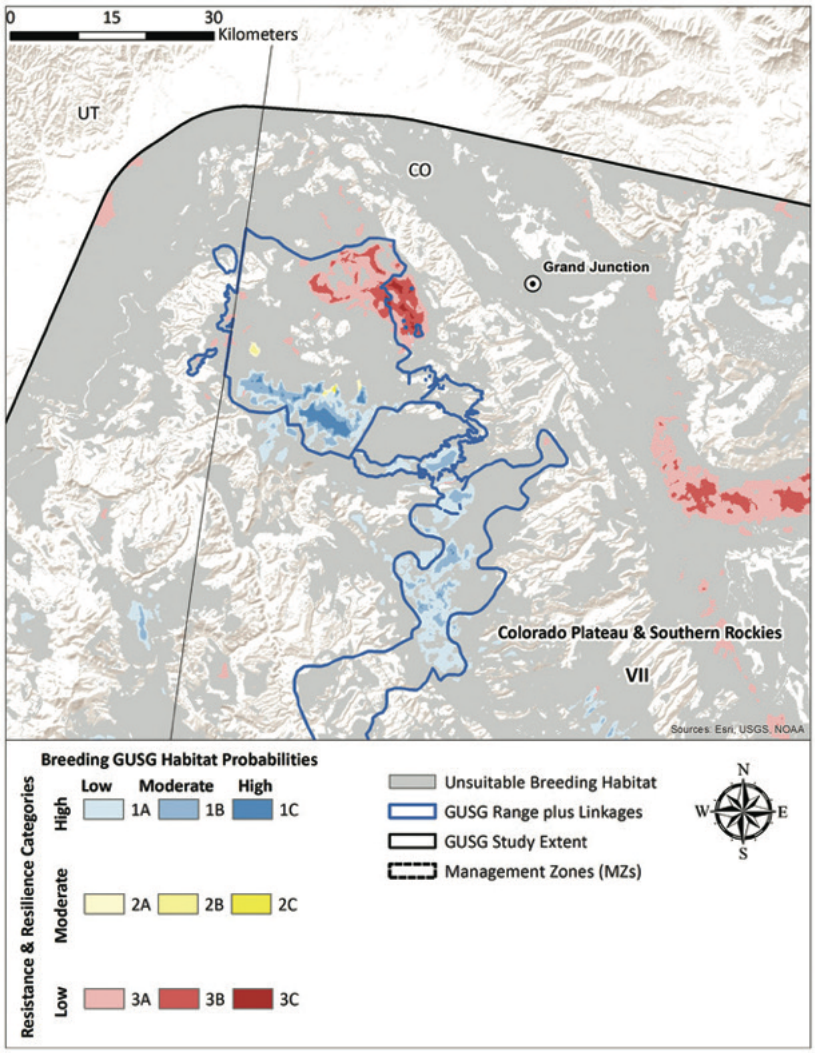
āURĦNj□ —Surface land management for an area in the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) with piñon and juniper expansion (Mesa County, Colorado) (BLM 2015).

In areas with high habitat probabilities that occur adjacent to breeding concentration centers or that could increase connectivity, management activities may include (1) targeted tree removal in early to mid-phase (Phase I and II) post-settlement piñon and juniper expansion areas to maintain or increase shrub/perennial herbaceous cover and decrease fuel loads, and (2) targeted tree removal or thinning in later phase (Phase III) post-settlement piñon and juniper to decrease possibility of high severity fire. Following tree removal or thinning, relatively cool and moist areas with moderate to high resilience and resistance and residual understories of perennial grasses and shrubs are often capable of unassisted recovery after either treatment or disturbance. However, relatively warm and dry areas with low resilience and resistance may not recover in a reasonable amount of time and may be susceptible to invasion by nonnative annual grasses and other weeds. If post treatment areas lack sufficient perennial native vegetation to promote recovery, they can be seeded with perennial grasses and forbs with capacity to persist and stabilize ecosystem processes under altered disturbance regimes and in a warming environment.



aLB(4 —Conifer-dominated ecological systems (USGS 2014) for an area in the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) with piñon and juniper expansion (Mesa County, Colorado). The dark brown colors represent conifer-dominated systems with the potential to expand into sagebrush-dominated systems (USDI BLM 2014).

Posttreatment seeding or postfire rehabilitation in low resilience and resistance areas may require more than one intervention for restoration success. This situation occurs in sage-grouse habitat along the Utah-Colorado border in the area known as Fish Park, where two fires recently occurred. In 1999, 3,580 ac (14.5 km^2) burned and in 2006, a second fire burned an additional 1,400 ac (5.7 km^2), of which 543 ac (2.2 km^2) overlapped the first fire. Even with postfire rehabilitation treatments, invasion of nonnative annual grasses occurred and additional intervention is now necessary. Establishing sagebrush is often challenging in these warm and dry areas with low resilience and resistance and the Bureau of Land Management is currently conducting trials to ascertain the best procedure to reestablish sagebrush (Heidi Plank, Colorado BLM, Grand Junction Field Office, personal communication). Seeding of introduced species, in this case western wheatgrass, can retard recovery of native perennial grasses and forbs that are important to sage-grouse and should be avoided in these types of areas (e.g., Lesica et al. 1996).



āURĦNj□ —Gunnison sage-grouse breeding habitat probabilities for the Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a) and surrounding area based on lek data from 1995 to 2015 intersected with resilience and resistance categories developed from the soil temperature and moisture regimes. The area is in Mesa County, Colorado and is exhibiting piñon and juniper expansion. The breeding habitat probabilities were developed for this report based on Doherty et al. 2016. The soil temperature and moisture regime data used in this report and the soil temperature and moisture regime categories are explained in Appendix 2. The relationships of the soil temperature and moisture regimes to the predominant ecological types are in table 3.

On the Piñon Mesa, areas with lower resilience and resistance and high to moderate breeding habitat probabilities, large, contiguous areas of sagebrush with intact understories are a high priority for conservation. In these areas, emphasis is on maintaining or increasing habitat conditions by minimizing stressors and disturbance. Appropriately managing livestock and recreational use in targeted areas is especially important to promote native perennial grass and forb growth and reproduction and to maintain or enhance resilience and resistance.

Historically, drought likely had a greater influence on tree dynamics than fire in this area (Shinneman and Baker 2009). However, in some areas of the northern Colorado plateau, a decline in piñon-juniper woodlands over the past century may have occurred due to an excess of fire since Euro-American settlement (Arendt and Baker 2013). Management aimed at restoring understory grasses and forbs has the potential to increase resilience and resistance to both drought and fire given climate warming. Monitoring can provide the necessary information to track change and adapt management.

(4MU64NUVRZVxexZ56UqjQZVZRjCjV6

Monitoring programs designed to track ecosystem changes in response to both stressors and management actions can be used to increase understanding of ecosystem resilience and resistance, realign management approaches and treatments, and implement adaptive management (Herrick et al. 2012; Reever-Morghan et al. 2006). Information is increasing on likely changes in sagebrush ecosystems undergoing additional stress and climate warming, but a large degree of uncertainty still exists. Currently, two consistent national monitoring efforts inventory vegetation and soil attributes and describe land health at the landscape scale: the Natural Resource Conservation Service, National Resource Inventory of non-Federal lands and the Bureau of Land Management, Landscape Monitoring Framework of public lands managed by the Bureau (part of the Bureau's Assessment Inventory and Monitoring strategy).

Strategic placement of monitoring sites and repeated measurements of ecosystem status and trends (e.g., ground cover, vegetation height, phase of tree expansion, soil and site stability) can be used to decrease uncertainty and increase effectiveness of management decisions (Rowland and Vojta 2013). Ideally, monitoring sites span environmental/productivity gradients and sagebrush ecological types that characterize sage-grouse habitat. Of particular importance are (1) ecotones between ecological types where changes in response to climate are expected to be largest (Loehle 2000; Stohlgren et al. 2000), (2) ecological types with climatic conditions and soils that are exhibiting nonnative species invasion and increased fire risk, and (3) ecological types with climatic conditions and soils that are exhibiting tree expansion and increased fire risk. Monitoring the response of sagebrush ecosystems to management treatments, including both pre and posttreatment data, is a first order priority because it provides information on treatment effectiveness that can be used to adjust methodologies.

Monitoring activities are most beneficial when standard approaches are used among and within agencies to collect, analyze, and report monitoring data (Rowland et al. 2013). Currently, effectiveness monitoring databases that are used by multiple agencies do not exist. However, several databases have been developed for tracking invasive species management and restoration/rehabilitation activities.

The National Fire Plan Operations and Reporting System is an interdepartmental and interagency database that accounts for hazardous fuel reduction, burned area rehabilitation, and community assistance activities. To our knowledge, this system is not capable of storing and retrieving the type of effectiveness monitoring information that is needed for adaptive management.

The FEAT FIREMON Integrated (https://www.frames.gov/partner-sites/ffi/ffi-home/) is a monitoring software tool designed to assist managers with collection, storage, and analysis of ecological information. It was constructed through a

complementary integration of the Fire Ecology Assessment Tool (FEAT) and Fire Effects Inventory and Monitoring Protocol (FIREMON). This tool allows the user to select among multiple techniques for effectiveness monitoring. If agencies agreed on effectiveness monitoring techniques, FEAT FIREMON databases with standard structures could be used in interagency effectiveness monitoring.

The Database for Inventory, Monitoring and Assessment (http://jornada.nmsu.edu/monit-assess/dima) is similar to FEAT FIREMON. This is a computer tablet-based data entry tool for field data entry directly into a database for later management and interpretation. This Microsoft Access database uses standardized plant nomenclature based on the current U.S. Department of Agriculture Plants Database. The data can be easily stored in the Land Treatment Digital Library (see below) to keep all treatment planning and implementation information together with the monitoring data. Also, the National Invasive Species Information Management System is designed to reduce redundant data entry regarding invasive species inventory, management, and effectiveness monitoring with the goal of providing information that can be used to determine effective treatments for invasive species. However, this tool is currently available only within the Bureau of Land Management.

Common databases can be used by agency partners to record and share monitoring data. The Land Treatment Digital Library (USGS 2015) provides a method of archiving and collecting common information for land treatments and might be used as a framework for data storage and retrieval. At present, interagency use is limited because of barriers affecting database access and data security. The Land Treatment Digital Library has demonstrated how this can work by accessing a variety of databases to populate useful information relating to land treatments.

To effectively evaluate treatments for adaptive management, the agencies involved will need to agree on monitoring methods and a common data storage and retrieval system. Once data can be retrieved, similar treatment projects can be evaluated to determine how well they achieve objectives for sage-grouse habitat, such as the criteria outlined in documents like the Habitat Assessment Framework (Stiver et al. 2006) or those in the GRSG example in Goldstein et al. (2013). Results of monitoring activities on treatment effectiveness are most useful when shared across jurisdictional boundaries, and several mechanisms are currently in place to improve information sharing (e.g., the Landscape Conservation Cooperatives, https://lccnetwork.org/; and Fire Science Exchange Projects, https://www.firescience.gov/JFSP_exchanges.cfm).

4HNEjP4G(ZVZRjCjV6oVG4NCZ6U4V

Several resources exist to assist in developing effective management strategies for persistent ecosystem threats. Archived information from the Center for Invasive Species Management website provides a variety of resources for managing nonnative invasive species, including information on individual species, planning and prioritizing threats, inventory and monitoring, ecologically based invasive plant management, control methods, prevention, restoration, and revegetation (http://www.weedcenter.org/). Also, a recent handbook on cheatgrass management is broadly applicable across the eastern portion of the range (Mealor et al. 2013). To address wildfire, invasive annual grasses, and conifer expansion in sagebrush ecosystems in the western portion of the range, field guides and handbooks have recently been developed that explicitly incorporate resilience and resistance concepts. These resources can be adapted to Management Zones II and VII to help

guide managers through the process of determining both the suitability of an area for treatment and the most appropriate treatment. Three treatment types are emphasized: (1) conifer removal (Miller et al. 2014), (2) post-fire rehabilitation (Miller et al. 2015), and (3) rehabilitation/restoration (Pyke et al., 2015a,b). Additional information on implementing these types of management treatments is synthesized in Monsen et al. (2004) and Pyke (2011); additional information on treatment response is synthesized in Miller et al. (2013).

Resources also exist to assist in addressing land use and development threats. Information is available on grazing management from university extension services at Montana State University (http://animalrangeextension.montana.edu/range/grazing-management.html), the University of Wyoming (Cagney et al. 2010), and Colorado State University (http://extension.colostate.edu/topic-areas/natural-resources/). Additional information on livestock management can be found at the national Grazing Lands Coalition website (http://www.grazinglands.org/) and Grass: The Stockman's Crop (http://agrilifecdn.tamu.edu/coastalbend/files/2015/02/Grass-The-Stockmans-Crop.pdf). Finally, the Federal land management agencies each have guidelines for livestock grazing.

A variety of programs exist to help support ranchers and enhance their ability to maintain rangelands as working lands. Long-term conservation easements are available through the Agricultural Conservation Easement Program that can help maintain large and intact sagebrush ecosystems by preventing cropland conversion and residential development (http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/easements/acep/). Also, financial and technical assistance is available for planning and implementing conservation practices that can improve ecological conditions and natural resources on rangelands through the Environmental Quality Incentives Program offered by the National Resource Conservation Service (http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/eqip/).

r4ME"HPU4MP

This report provides a strategic, multiscale approach for prioritizing areas for management and determining effective management strategies in the eastern portion of sagebrush biome. The focus is on addressing persistent ecosystem and land use and development threats to sagebrush ecosystems, GRSG, and GUSG. A highly similar approach was developed for the western portion of the range (Chambers et al. 2014a). That approach was subsequently incorporated into the "Greater Sage-Grouse Wildfire, Invasive Annual Grasses, and Conifer Expansion Assessment" (USDI BLM 2014), and served as the basis for a multi-year program of work by the BLM in the Great Basin.

The approaches developed for the western portion of the range (Chambers et al. 2014a) and for this report were used to develop an initial Science Framework (Chambers et al. 2016b) for the Conservation and Restoration Strategy of DOI Secretarial Order 3336 on Rangeland Fire Prevention, Management and Restoration (USDI 2015a,b). The Science Framework will ultimately include sections that relate specific management issues/activities (climate change, wildfire, nonnative invasive plant species, grazing practices, seed strategy considerations, monitoring, mitigation) to the approach developed for prioritizing areas for management and determining effective management strategies. Sections on wildfire and fuels

management and climate change were developed for this report and are included in Appendices 7 and 8 because they are central to the issues facing sagebrush ecosystems and sage-grouse.

The approach described in this report and in the Science Framework is intended to be adaptive. As new science and information are developed for sagebrush ecosystems and on sagebrush obligate species, they will be used to improve our ability to prioritize areas for management and determine effective management strategies.

References

kVKQ1KwD□ty/vDhCr1N31Nw/vvQQDNvDL□NKND□ /ZDQ1DNvDaLB1L□□ based approach for endangered Greater Sage-Grouse. Ecological Applications. 17: 508–526.

Aldridge, C.L; Hanser, S.E.; Nielsen, S.E.; [et al.]. 2011. Chapter 6: Detectability adjusted count models of songbird abundance. In: Hanser, S.E.; Leu, M.; Knick S.T.; [et al.], eds. Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Lawrence, KS: Allen Press: 141–220.

Aldridge, C.L.; Nielsen, S.E.; Beyer, H.L.; [et al.]. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions. 14: 983–994.

Aldridge, C.L.; Saher, D.J.; Childers, T.; [et al.]. 2012. Crucial nesting habitat for Gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management. 76: 391–406.

Allen, E.B.; Knight, D.K. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. The Southwestern Naturalist. 29: 407–421.

Alexander, E.B.; Mallory, J.I.; Colwell, W.L. 1993. Soil-elevation relationships on a volcanic plateau in the southern Cascade Range, northern California, USA. Catena. 20: 113–128.

Anderson, A.B.; Jenkins, C.N. 2006. Applying nature's design: corridors as a strategy for biodiversity conservation. New York, NY: Columbia University Press. 256 p.

Arendt, P.A.; Baker, W.L. 2013. Northern Colorado Plateau piñon-juniper woodland decline over the past century. Ecosphere. 4(8): 103.

Arredondo, J.T.; Jones, T.A.; Johnson, D.A. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. Journal of Range Management. 51: 584–589.

Bainbridge, D.A. 2007. A guide for desert and dryland restoration. Washington, DC: Island Press and Society for Ecological Restoration International. 391 p.

pZIjNvdcNjmHN4eCjNUEZVZVxNjEjV6NjUVPZRjONHPSjE4P8P6jCP6V□ Knick S.T., Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 185–201.

Baker, W.H; Shinneman, D.J. 2004. Fire and restoration of piñon-juniper woodlands in the western United States: A review. Forest Ecology and Management. 189: 1–21.

Bakker, J.D.; Wilson, S.D.; Christian, J.M.; [et al.]. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications. 13: 137–153.

Barbour, R.J.; Hemstrom, M.A.; Hayes, J.L. 2007. The Interior Northwest Landscape Analysis System: A step toward understanding integrated landscape analysis. Landscape and Urban Planning. 80: 333–344.

Barker, W.T.; Whitman, W.C. 1988. Vegetation of the Northern Great Plains. Rangelands. 6: 266–272.

Baruch-Mordo, S.; Evans, J.S.; Severson, J.P.; [et al.]. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. Biological Conservation. 167: 233–241.

pZPIUVsqpZPIUVmE4"4R4GRjNCUVZ6U4MZVx47 jNUVRUV6Sj7jjx87UV6jN annual grass *Bromus japonicus*. Journal of Range Management. 34: 369–372.

pjEIsqU6ESj"tbMHjVEjP4G"UqjP64EIRNZLU VR4MPZRjRN4HPjSZOU6Z6 Wildlife Society Bulletin. 28: 993–1002.

Beck, J.L.; Connelly, J.W.; Wambolt, C.L. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management. 65: 444–455.

Beck, J.L.; Reese, K.; Connelly, J.W.; [et al.]. 2006. Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin. 34: 1070–1078.

Bergquist, E.; Evangelista, P.; Stohlgren, T.J.; [et al.]. 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environmental Monitoring and Assessment. 128: 381–394.

Bestelmeyer, B.T.; Tugel, A.J.; Peacock, G.L.J.; [et al.]. 2009. State-and-transition models for heterogeneous landscapes: A strategy for development and application. Rangeland Ecology and Management. 62: 1–15.

Blank, R.S.; Morgan, T. 2012. Suppression of *Bromus tectorum* L. by established perennial grasses: Potential mechanisms—Part One. Applied Environmental Soil Science. 2012: Article ID 632172. 9 p. doi:10.1155/2012/632172. https://www.hindawi.com/journals/aess/2012/632172/

Blus, L.J.; Staley, C.S.; Henny, C.J.; [et al.]. 1989. Effects of organophosphorus insecticides on sage grouse in southeastern Idaho. The Journal of Wildlife Management. 53: 1139–1146.

Booth, M.S.; Caldwell, M.M.; Stark, J.M. 2003. Overlapping resource use in three Great Basin species: Implications for community invasibility and vegetation dynamics. Journal of Ecology. 91: 36–48.

Borell, A.E. 1939. Telephone wires fatal to sage grouse. Condor. 41(1): 85–86.

Boyd, C.S.; Svejcar, T.J. 2009. Managing complex problems in rangeland ecosystems. Rangeland Ecology and Management. 62: 491–499.

Boyd, C.S.; Beck J.L.; Tanaka, J. 2014a. Livestock grazing and sage-grouse habitat: Impacts and opportunities. Journal of Rangeland Applications. 1: 58–77.

Boyd, C.S.; Johnson, D.D.; Kerby, J.D.; [et al.]. 2014b. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? Rangeland Ecology and Management. 67: 358–368.

Bradford, J.B.; Lauenroth, W.K. 2006. Controls over invasion of *Bromus tectorum*: The importance of climate, soil, disturbance and seed availability. Journal of Vegetation Science. 17: 693–704.

Bradley, B.A. 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology. 15: 196–208.

Bradley, B.A. 2010. Assessing ecosystem threats from global and regional change: Hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography. 33: 198–208.

Bradley, B.A.; Curtis, C.A.; Chambers, J.C. 2016. *Bromus* response to climate and projected changes with climate change. In: Germino, M.J.; Chambers, J.C.; Brown, C.S., eds. Exotic brome-grasses in arid and semi-arid ecosystems of the Western US: Causes, consequences and management implications. New York, NY: Springer: 257–274.

Bragg, T.B.; Steuter, A.A. 1996. Prairie ecology—The mixed grass prairie. In: Samson, F.B.; Knopf, F.L., eds. Prairie conservation—Preserving North America's most endangered ecosystem. Washington, DC: Island Press: 53–66.

Braun, C.E.; Oedekoven, O.O.; Aldridge, C.L. 2002. Oil and gas development in western North America: Effects on sagebrush steppe avifauna with particular emphasis on sage-grouse. Transactions of the North American Wildlife and Natural Resources Conference. 67: 337–349.

Braun, C.E.; Oyler-McCance, S.J.; Nehring, J.A.; [et al.]. 2014. The historical distribution of Gunnison Sage-grouse in Colorado. The Wilson Journal of Ornithology. 126: 207–217.

Briske, D.D.; Richards, J.H. 1995. Plant responses to defoliation: A physiological, morphological, and demographic evaluation of individual plants to grazing: Current P6Z6HPZVxjE4"4RUEZ"PURVUEZVEjoVpjxHVZSs4PjQjjxPvU"x"ZVx5"ZV6P□ Physiological ecology and developmental morphology. Denver, CO: Society for Range Management: 635–710.

Briske, D.D.; Bestelmeyer, B.T.; Stringham, T.K.; [et al.]. 2008. Recommendations for development of resilience-based state-and-transition models. Rangeland Ecology and Management. 61: 359–367.

Briske, D.D.; Fuhlendorf, S.D.; Smeins, F.E. 2005. State-and-transition models, thresholds, rangeland health: A synthesis of ecological concepts and perspectives. Rangeland Ecology and Management. 58: 1–10.

Briske, D.D.; Sayre, N.F.; Huntsinger, L.; [et al.]. 2011. Origin, persistence, and resolution of the rotational grazing debate: Integrating human dimensions into rangeland research. Rangeland Ecology and Management. 64: 325–334.

Brooks, M.L.; Brown, C.S.; Chambers, J.C.; [et al.]. 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western U.S. In: Germino, M.J.; Chambers, J.C.; Brown, C.S., eds. Exotic brome-grasses in arid and semiarid ecosystems of the western U.S. New York, NY: Springer: 11–60.

Brooks, M.L.; Matchett, J.R.; Shinneman, D.J.; [et al.]. 2015. Fire patterns in the range of Greater Sage-Grouse, 1984–2013—implications for conservation and management. Open-File Report 2015-1167, U.S. Geological Survey. 66 p. http://dx.doi.org/10.3133/ofr20151167. [Accessed June 13, 2016].

and management in Wyoming's Greater Sage-Grouse habitat. Extension Bulletin B-1203. Laramie, WY: University of Wyoming, College of Agriculture.

Carwardine, J.; O'Connor, T.; Legge, S.; [et al.]. 2011. Priority threat management to protect Kimberley wildlife. Brisbane, Australia: CSIRO Ecosystem Sciences.

Caudle, D.; DiBenedetto, J.; Karl, M.; [et al.]. 2013. Interagency ecological site InteragencyEcolSiteHandbook.pdf. [Accessed June 13, 2016].

Chambers, J.C.; Beck, J.L.; Campbell, S.; [et al.]. 2016b. Science Framework for the Conservation and Restoration Strategy of the Department of Interior Secretarial Order 3336. Using resilience and resistance concepts to assess threats to sagebrush ecosystems and sage-grouse, prioritize conservation and restoration actions, and inform management strategies. Version I. August 5, 2016. Unnumbered Publication. Fort Collins, CO: U.S Department of Agriculture, Forest Service, Rocky Mountain Research Station. 202 p.

Chambers, J.C.; Bradley, B.A.; Brown, C.A.; [et al.]. 2014b. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in the cold desert shrublands of western North America. Ecosystems. 17: 360–375.

Chambers, J.C.; Germino, M.J.; Belnap, J.; [et al.]. 2016a. Plant community resistance to invasion by Bromus species--the role of community attributes, Bromus interactions with plant communities and Bromus traits. In: Germino, M.J., Chambers, J.C., Brown, C.S., eds. Exotic brome-grasses in arid and semiarid ecosystems of the western U.S. New York, NY: Springer: 275–306.

Chambers, J.C.; Miller, R.F.; Board, D.I.; [et al.]. 2014c. Resilience and resistance of sagebrush ecosystems: Implications for state and transition models and management treatments. Rangeland Ecology and Management. 67: 440–454.

Chambers, J.C.; Pyke, D.A.; Maestas, J.D.; [et al.]. 2014a. Using resistance and resilience ecosystem and sage-grouse—A strategic multi-scale approach. Gen. Tech. Rep. RMRS-GTR-326. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 73 p.

Chambers, J.C.; Roundy, B.A.; Blank, R.R.; [et al.]. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs. 77: 117–145.

Chen, I.C.; Hill, J.K.; Ohlemueller, R.; [et al.]. 2011. Rapid range shifts of species associated with high levels of climate warming. Science. 333: 1024–1026.

Coates, P.S.; Casazza, M.L.; Blomberg, E.J.; [et al.]. 2013. Evaluating Greater Sage-Grouse seasonal space use relative to leks: Implications for surface use designations in sagebrush ecosystems. Journal of Wildlife Management. 77: 1598–1609.

Coates, P.S.; Casazza, M.L.; Ricca, M.A.; [et al.]. 2016. Integrating spatially explicit indices of abundance and habitat quality: An applied example for Greater Sage-Grouse management. Journal of Applied Ecology. 53: 83–95.

differential habitat use of nesting buteos and ravens within sagebrush ecosystem:

Implications for transmission line development. Condor: Ornithological Applications. 116: 341–356.

Collins, S.L., Uno, G.E. 1985. Seed predation, seed dispersal, and disturbance in grasslands: A comment. American Naturalist. 125: 866–872.

Commons, M.L.; Baydack, R.K.; Braun, C.E. 1999. Sage grouse response to pinyon-juniper management. In: Monsen, S.B.; Stevens, R., comps. Proceedings: Ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proceedings RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 238–239.

r4VxVGUPOjNRdSZCOjNPsOU46UEZVxOU46UEUVHjVEjP4V *Bromus tectorum* invasion and *Artemisia tridentata*

Wildland Fire. 20: 1–8.

Connelly, J.W.; Hagen, C.A.; Schroeder, M.A. 2011a. Characteristics and dynamics of Greater Sage-Grouse populations. In: Knick, S.T.; Connelly J.W., eds. Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 53–68.

Connelly, J.W.; Knick, S.T.; Schroeder, M.A.; [et al.]. 2004. Conservation assessment of

Association of Fish and Wildlife Agencies, Cheyenne, WY. 610 p.

Connelly, J.W.; Rinkes, E.T.; Braun, C.E. 2011b. Characteristics of Greater Sage-Grouse habitats: A landscape species at micro and macro scales. In: Knick, S.T.; Connelly, J.W., eds. Greater Sage-Grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 69–84.

Connelly, J.W.; Schroeder, M.A.; Sands, A.R.; [et al.]. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin. 28(4): 967–985.

Cook, J.G.; Irwin, L.L. 1992. Climate-vegetation relationships between the Great Plains and Great Basin. American Midland Naturalist. 127: 316–326.

Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: Adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden. 72: 852–863.

Curtain, C.G.; Parker, J.P. 2014. Foundations of resilience thinking. Conservation Biology. 4: 912–923.

Cushman, S.A.; Mersmann, T.J.; Moisen, G.G.; [et al.]. 2013. Using habitat models for habitat mapping and monitoring. Chapter 5. In: Rowland, M.M.; Vojta, C.D., tech. eds. 2013. A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-GTR-89.

14 p.

Dahlgren, R.A.; Boettinger, J.L.; Huntington, G.L.; [et al.]. 1997. Soil development along an elevational transect in the western Sierra Nevada. Geoderma. 78: 207–236.

D'Antonio, C.M.; Thomsen M. 2004. Ecological resistance in theory and practice. Weed Technology. 18: 1572–1577.

David, E. 2013. Innovative snow harvesting technology increases vegetation establishment success in native sagebrush ecosystem restoration. Plant and Soil. 373: 843–856.

Davies, G.M.; Bakker, J.D.; Dettweiler-Robinson, E.; [et al.]. 2012. Trajectories of change
UVPZRjONHPSP6j55jqjRj6Z6U4VE4CCHVU6UjPUVNj"Z6[illegible]
Applications. 22: 1562–1577.

Dinkins, J.B.; Conover, M.R.; Kirol, C.P.; [et al.]. 2012. Greater Sage-Grouse (*Centrocercus urophasianus*) select nest-sites and brood-sites away from avian predators. The Auk. 129: 600–610.

Dinkins, J.B.; Conover, M.R.; Kirol, C.P.; [et al.]. 2014a. Greater Sage-Grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. The Condor: Ornithological Applications. 116: 629–642.

Dinkins, J.B.; Conover, M.R.; Kirol, C.P.; [et al.]. 2014b. Greater Sage-Grouse hen survival: Effects of raptors, anthropogenic and landscape features, and hen behavior. Canadian Journal of Zoology. 92: 319–330.

Dinkins, J.B.; Smith, K.T.; Beck, J.L.; [et al.]. 2016. Microhabitat conditions in Wyoming's sage-grouse Core Areas: Effects on nest site selection and success. PLoS ONE. 11(3): e0150798.

Doherty, K.E.; Beck, J L.; Naugle, D.E. 2011. Comparing ecological site descriptions
64SZOU6Z6ESZNZE6jNUP6UEPUVHjVEUVRyNjZ6jN+ZRPV64HFjMJP6jVEjZVx
success. Rangeland Ecology and Management. 64(4): 344–351.

Doherty, K.E.; Evans, J.S.; Coates, P.S. [et al.]. 2016. Importance of regional variation in conservation planning: A range-wide example of the Greater Sage-grouse. Ecosphere. 7: Article e01462.

Doherty, K.E.; Naugle, D.E.; Tack, J.D.; [et al.]. 2014. Linking conservation actions to demography: Grass height explains variation in Greater Sage-Grouse nest survival. Wildlife Biology. 20: 320–325.

Doherty, K.E.; Naugle, D.E.; Walker, B.L. 2010a. Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management. 74: 1544–1553.

Doherty, K.E.; Naugle, D.E.; Walker, B.L.; [et al.]. 2008. Greater Sage-Grouse winter habitat selection and energy development. Journal of Wildlife Management. 72: 187–195.

Doherty, K.E.; Tack, J.D.; Evans, J.S.; Naugle, D.E. 2010b. Mapping breeding densities of Greater Sage-Grouse: a tool for range-wide conservation planning. BLM completion report: Agreement # L10PG00911. U.S. Department of the Interior, Bureau of Land Management. 31 p.

Donnelly, P.; Tack, J.D.; Doherty, K.E.; [et al.]. [In press]. Extending conifer removal and landscape protection strategies from sagegrouse to songbirds, a rangewide assessment. Rangeland Ecology.

Duncan, M.B. 2010. Sage-grouse and coal-bed methane: Can they coexist within the Powder River Basin? Journal of Natural Resources and Life Sciences. 39: 53–62.

Eckert, R.E.; Peterson, F.F.; Meurisse, M.S.; [et al.]. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. Journal Range Management. 39: 414–420

Eisenhart, K.S. 2004. Historic range of variability and stand development in piñon-juniper woodlands of western Colorado. Dissertation. Boulder: University of Colorado. 239 p.

Evans, D.; Goble, D.D.; Scott, J.M. 2013. New priorities as the Endangered Species Act turns 40. Frontiers in Ecology and the Environment. 11: 519.

Evans, J.S.; Murphy, M.A. 2014. rfUtilities. R package version 10-0, http://cran.r-project.org/package=rfUtilities. [Accessed June 13, 2016].

Falkowski, M.J.; Evans, J.S.; Naugle, D.E.; [et al.]. [In Press]. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management.

Fedy, B.C.; Aldridge, C.L.; Doherty, K.E.; [et al.]. 2012. Interseasonal movements of Greater Sage-Grouse migratory behavior and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management. 76: 1062–1071.

Fedy, B.C.; Doherty, K.E.; Aldridge, C.L.; [et al.]. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: An example using Greater Sage-Grouse in Wyoming. Wildlife Monographs. 190: 1–39.

Field, S.A.; Tyre, A.J.; Jonzen, N.; [et al.]. 2004. Minimizing the cost of environmental management decisions by optimizing statistical thresholds. Ecology Letters. 7: 669–675.

Finch, D.M.; Pendleton, R.L.; Reeves, M.C.; [et al.]. 2016. In: Vose, J.M.; Clark, J.S.; Luce, C.H.; [et al.], eds. Effects of drought on forests and rangelands in the United States: A comprehensive science synthesis. Gen. Tech. Rep. WO-93b. Washington, DC: U.S.
ij5ZN6CjV64GeRNUEH”6HNja4NjP6+jNqUEjvZPSUVR64VjGEj□

Finn, S.P.; Knick, S.T. 2011 Changes to the Wyoming Basins landscape from oil and natural gas development. In: Hanser, S.E.; Leu, M.; Knick, S. T.; [et al.], eds. Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Lawrence, KS: Allen Press: 69–87.

Finney, M.A.; McHugh, C.W.; Grenfell, I. 2010. Continental-scale simulation of burn
5N4OZOU”U6UjPZCj”jVR6SPZVxNjPULjxUP6NUOH6U4VRQ4N6SZ6jPoVdUjRZPb□
jxa4HN6SUV6jNVZ6U4VZ”E4VGjNjVEj4VG4NjP6NjNjPjZNH8jCOjN4UCONZ□
Portugal. Associacao para o Desenvolvimento da Aerodinamica Industrial. 12 p.

Fischer, J.; Peterson G.D.; Gardner T.A.; [et al.]. 2009. Integrating resilience thinking and optimisation for conservation. Trends in Ecology and Evolution. 24: 549–554.

a”48x(tuZVVZig4CCjvuuUP64NUEZ”ZVxNjEjV6NjNjRUCjPUV5U+4V□
juniper woodlands on Mesa Verde, Colorado, USA. Forest Ecology and Management. 198: 269–289.

Floyd, M.L.; Hanna, D.; Romme, W.H.; [et al.]. 2004. Predicting and mitigating weed
UVqZPU4VP64NjP64NjVZ6HNZ”54P6NjPHEEjPPU4VUVjPZdjNxjIZ6U4VZ”cZNIf4”4NZx4□
USA. International Journal of Wildland Fire. 15: 247–259.

Folke, C.; Carpenter, S.; Walker, B.; [et al.]. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology and Systematics. 35: 557–581.

Forbis, T.A.; Provencher, L.; Frid, L.; [et al.]. 2006. Great Basin land management planning using ecological modeling. Environmental Management. 38: 62–83.

Franco, A.M.A.; Hill, J.K.; Kitschke, C.; [et al.]. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biology. 12: 1545–1553.

Freilich, J.E.; Emlen, J.M.; Duda, J.J.; [et al.] 2003. Ecological effects of ranching: A six-point critique. BioScience. 53: 759–765.

Fuhlendorf, S.D.; Engle, D.M. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. BioScience. 51: 625–632.

Gelbard, J.L.; Belnap, J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology. 17: 420–432.

Gibson, D.; Bomberg, E.J.; Sedinger, J.S. 2016. Evaluating vegetation effects on animal demographics: The role of plant phenology and sampling bias. Ecology and Evolution. 6(11): 3621–3631. http://onlinelibrary.wiley.com/doi/10.1002/ece3.2148/full.

Goble, D.D.; Wiens, J.A.; Scott, J.M.; [et al.]. 2012. Conservation-reliant species. Bioscience 62: 869–873.

Goldstein, M.I.; Suring, L.H.; Vojta, C.D.; [et al.]. 2013. Developing a habitat monitoring program: Three examples from National Forest planning. Chapter 10. In: Rowland, M.M.; Vojta, C.D., tech. eds. 2013. A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-GTR-89. Washington, DC: U.S. Department of Agriculture, Forest

Greb, B.W. 1980. Snowfall and its potential management in the semiarid central Great Plains. ARM-W-18. Oakland, CA: U.S. Department of Agriculture, Agricultural and Research, Western Region, Science and Education Administration. 64 p.

Gregory, A.J.; Beck, J.L. 2014. Spatial heterogeneity in response of male Greater Sage-Grouse lek attendance to energy development. PLoS ONE. 9(6): e97132.

Descriptions. May 11, 2010 Version. https://archive.epa.gov/wed/ecoregions/web/html/na_eco.html#Level III. [Accessed June 13, 2016].

Gunnison Sage-grouse Rangewide Steering Committee [GSGRSC]. 2005. Gunnison sage-grouse rangewide conservation plan. Denver, CO: Colorado Division of Wildlife. 490 p.

Hagen, C.A.; Connelly, J.W.; Schroeder, M.A. 2007. Meta-analysis of Greater Sage-Grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology. 13(sp1): 42–50.

Hanser, S.E.; Knick, S.T. 2011. Greater Sage-Grouse as an umbrella species for shrubland passerine birds: A multiscale assessment. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 473–487.

Hanser, S.E.; Leu, M.; Knick S.T.; Aldridge, C.L., eds. 2011. Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Lawrence, KS: Allen Press. 429 p.

Harju, S.M.; Dzialak, M.R.; Taylor, R.C.; [et al.]. 2010. Thresholds and time lags in the effects of energy development on Greater Sage-Grouse populations. Journal of Wildlife Management. 74: 437–448.

Hart, C.R.; Carpenter, B.B. 2005. Stocking rate and grazing management. Rangeland Drought Management for Texans E-64: 05- 01. College Station, TX: Texas Agricultural Experiment Station. 3 p.

Havens, K.; Vitt, P.; Still, S.; [et al.]. 2015. Seed sourcing for restoration in an era of climate change. Natural Areas Journal. 35: 122–133.

Herman-Brunson, K.M.; Jensen, K.C.; Kaczor, N.W.; [et al.]. 2009. Nesting ecology of Greater Sage-Grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology. 15: 237–246.

Herrick, J.E.; Duniway, M.C.; Pyke, D.A.; [et al.]. 2012. A holistic strategy for adaptive land management. Journal of Soil and Water Conservation. 67: 105A–113A.

Hess, J.E.; Beck, J.L. 2012a. Burning and mowing Wyoming big sagebrush: Do treated sites meet minimum guidelines for Greater Sage-Grouse breeding habitats? Wildlife Society Bulletin. 36: 85–93.

ujPPsmpjEIsfOiUP6HNOZVEjGZE64NPUVHjVEUVRyN jZ6jN-ZRjyN4HPjjI
abandonment in northcentral Wyoming. Journal of Wildlife Management. 76: 1625–1634.

Hobbs, R.J.; Higgs, E.; Harris, J.A. 2009. Novel ecosystems: Implications for conservation and restoration. Trends in Ecology and Evolution. 24: 599–605.

Hockett, G.A. 2002. Livestock impacts on the herbaceous components of sage grouse habitat: A review. Intermountain Journal of Sciences. 8: 105–114.

Holling, C.S. 1973. Resilience and stability in ecological systems. Annual Review of Ecology and Systematics. 4: 1–23.

Holloran, M.J.; Anderson, S.H. 2005. Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. Condor. 107: 742–752.

Holloran, M.J.; Heath, B.J.; Lyon, A.G.; Slater , S.J.; [et al.]. 2005. Greater Sage-Grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management. 69:

Holmes, A.A.; Miller, R.F. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. Journal of Wildlife Management. 74: 1834–1840.

Homer, C.G.; Xian, X.; Aldridge, C.L.; [et al.]. 2015. Forecasting sagebrush ecosystem components and Greater Sage-Grouse habitat for 2050: Learning from past climate patterns and Landsat imagery to predict the future. Ecological Indicators. 55: 131–145.

Howe, K.B.; Coates P.S.; Delehanty D.J. 2014. Selection of anthropogenic features and vegetation characteristics by nesting common ravens in the sagebrush ecosystem. Condor: Ornithological Applications. 116: 35–49.

Interagency Greater Sage-Grouse Disturbance and Monitoring Subteam [IGSDMS]. 2014. The Greater Sage-Grouse monitoring framework. Washington, DC: U.S. Department of the Interior, Bureau of Land Management; U.S. Department of Agriculture, Forest Service. S665PJ5"ZVVUVRO"CR4qj5"GN4V64GEj5N4"jE6P"H5
GRSG-FINAL-Monitoring_Framework_20140530.pdf. [Accessed June 25, 2016].

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin. 83: 215–236.

James, J.J.; Drenovsky, R.A.; Monaco, T.A.; [et al.]. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: Effective strategy or incomplete framework? Ecological Applications. 21: 490–502.

Jetz, W.; Wilcove, D.S.; Dobson, A.P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology. 5: 1211–1219.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61: 65–71.

Johnson D.D.; Miller, R.F. 2006. Structure and development of expanding western juniper 744x”ZVxPZPUVHjVEjxO8674645 4RNZ5SUEqZNUZO”jPs4NjP68ZVx(ZVZRjCjV6□ 229: 7–15.

s4SVP4Vyg+4NjVP4Vaa#6r”ZUNspwj6Z”3cZEUE14N6S7jP6G4NjP66Njj□ seed zones: A template for native plants? Native Plants Journal. 5: 131–140.

Kaltenecker, J.H.; Wicklow-Howard, M.; Pellant, M. 1999. Biological soil crusts: Natural barriers to *Bromus tectorum* L. establishment in the northern Great Basin, USA. In: Eldridge D.; Freudenberger D., eds. People and rangelands: building the future: Proceedings of the VI International Rangeland Congress; 1999 July 19–23; Queensland, Australia. Aitkenvale, Queensland: International Rangeland Congress, Inc.: 109–111.

Kirol, C.P.; Beck, J.L.; Dinkins, J.B.; [et al.]. 2012. Microhabitat selection for nesting and brood rearing by the Greater Sage-Grouse in xeric big sagebrush. The Condor. 114: 75–89.

Kirol, C.P.; Beck, J.L.; Huzurbazar, S.V.; [et al.]. 2015a. Identifying Greater Sage-Grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications. 25: 968–990.

Kirol, C.P.; Sutphin, A L.; Bond, L.; Fuller, M.R.; Maechtle, T.L. 2015b. Mitigation jGGjE6UqjVjPPG4NUC5N4qUVRVjP6UVRPHEEjPP4GyNjZ6jN+ZRjyN4HPjUVHjVEjxO8jVjNR8□ development. Wildlife Biology. 21: 98–109.

Knapp, P.A. 1996. Cheatgrmonsenass (*Bromus tectorum*) dominance in the Great Basin Desert. Global Environmental Change. 6: 37–52.

Knick, S.T. 2011. Historical development, principal Federal legislation, and current management of sagebrush habitats—Implications for conservation. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 13–31.

Knick, S.T.; Connelly, J.W. 2011. Greater Sage-Grouse and sagebrush—An introduction to the landscape. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 1–9.

fVUEI+zbZVPjN+m(U”jNgawj6Z”3mE4”4RUEZ”UVHjVEjZVx5Z6S7Z8P□ of land use in sagebrush. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 203–251.

Knick, S.T.; Hanser, S.E.; Preston, K.L. 2013. Modeling ecological minimum requirements for distribution of Greater Sage-Grouse leks: Implications for population connectivity across their western range, U.S.A. Ecology and Evolution. 3: 1539–1551.

Knight, D.H.; Jones, G.P.; Reiners, W.A.; [et al.]. 2014. Mountains and plains: The ecology of Wyoming landscapes. Second edition. New Haven, CT: Yale University Press. 404 p.

Knopf, F.L. 1996. Prairie legacies—Birds. In: Samson, F.B., Knopf, F.L., eds. Prairie conservation—Preserving North America’s most endangered ecosystem. Washington, DC: Island Press: 135–148.

Knowles, N.; Dettinger, M.D.; Cayan, D.R. 2006. Trends in snowfall versus rainfall in the Western United States. Journal of Climate. 19: 4545–4559.

Kunkel, K.E.; Stevens, L.E.; Stevens, S.E.; [et al.]. 2013a. Regional climate trends and scenarios for the U.S. national climate assessment. Part 4. Climate of the U.S. Great Plains, NOAA Tech. Rep. NESDIS 142-4. Washington, DC: U.S. Department of Commerce, Oceanic and Atmospheric Administration . 82 p.

Kunkel, K.E.; Stevens, L.E.; Stevens, S.E.; [et al.]. 2013b. Regional climate trends and scenarios for the U.S. national climate assessment. Part 5. Climate of the Southwest U.S., NOAA Tech. Rep. NESDIS 142-5. Washington, DC: U.S. Department of Commerce, Oceanic and Atmospheric Administration . 79 p.

Lauenroth, W.K.; Schlaepfer, D.R.; Bradford, J.B. 2014. Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. Ecosystems. 17: 1469–1479.

LeBeau, C.W.; Beck, J.L.; Johnson, G.D.; [et al.]. 2014. Short-term impacts of wind energy [illegible] 522–530.

Lemoine, N.; Bauer, H.G.; Peintinger, M.; [et al.]. 2007. Effects of climate and land-use change on species abundance in a central European bird community. Conservation Biology. 21: 495–503.

Leonard, K.M.; Reese, K.P.; Conelly, J.W. 2000. Distribution, movements, and habitats of sage grouse *Centrocercus uro- phasianus* on the Upper Snake River Plain of Idaho: Changes from the 1950's to the 1990's. Wildlife Biology 6: 265–270.

Lesica, P.; Deluca, T.H. 1996. Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. Journal of Soil and Water Conservation. 51: 408–409.

[illegible] patterns: Implications for sage-grouse conservation. In: Knick, S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 253–272.

[illegible] the western U.S. ecoprovinces, 1916–2003. Ecological Applications. 19: 1003–1021.

Lockwood, J.A.; DeBrey, L.D. 1990. A solution for the sudden and unexplained extinction of the Rocky Mountain Grasshopper (Orthoptera: Acrididae). Environmental Entomology. 19: 1194–1205.

Loehle, C. 2000. Forest ecotone response to climate change: Sensitivity to temperature response functional forms. Canadian Journal of Forest Research. 30: 1362–1645.

Lyon, A.G.; Anderson, S.H. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin. 31(2): 486–491.

Mack, R.N.; Pyke, D.A. 1983. Demography of *Bromus tectorum*: Variation in time and space. Journal of Ecology. 71: 69–93.

Mack, R.N.; Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist. 119: 757–773.

Maddox, J.G. 1937. The Bankhead-Jones Farm Tenant Act. Law and Contemporary Problems. 4(4): 434–455.

Maestas, J.D.; Campbell, S.B.; Chambers, J.C.; [et al.]. 2016. Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. Rangelands. 38: 120–128.

Maestas, J.D.; Knight, R.L.; Gilgert, W.C. 2003. Biodiversity across a rural land-use gradient. Conservation Biology. 17: 1425–1434.

Malainey, M.E.; Sherriff, B.L. 1996. Adjusting our perceptions: Historical and archaeological evidence of winter on the plains of Western Canada. Plains Anthropologist. 41:333–357.

Manier, D.J.; Aldridge, C.L.; Anderson, P.J.; [et al.]. 2011. Land use and habitat conditions across the southwestern Wyoming sagebrush steppe: Development impacts, management effectiveness and the distribution of invasive plants. Natural Resources and Environmental Issues. 17: Article 4. http://digitalcommons.usu.edu/nrei/vol17/iss1/4. [Accessed June 13, 2016].

Manier, D.J.; Aldridge, C.L.; O'Donnell, M.; [et al.]. 2014. Human infrastructure and invasive plant occurrence across rangelands of Southwestern Wyoming, USA. Rangeland Ecology and Management. 67: 170–172.

Manier, D.J.; Wood, D.J.A.; Bowen, Z.H.; [et al.]. 2013. Summary of science, activities, [illegible] (*Centrocercus urophasianus*). Open-File Report 2013-1098. Washington, DC: U.S. Department of the Interior, U.S. Geological Survey. 297 p.

Mantyka-Pringle, C.S.; Martin, T.G.; Rhodes, J.R. 2011. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology. 18(4): 1239–1252. doi: 10.1111/j.1365-2486.2011.02593.x.

[illegible] *Bromus tectorum*) invasion at high elevation in Wyoming. Invasive Plant Science and Management. 5: 427–435.

Mealor, B.A.; Mealor, R.D.; Kelley, W.K.; [et al.]. 2013. Cheatgrass management handbook: Managing an invasive annual grass in the Rocky Mountain Region. Laramie, WY: University of Wyoming; Fort Collins, CO: Colorado State University. 131 p.

Meinke, C.W.; Knick, S.T.; Pyke, D.A. 2009. A spatial model to prioritize sagebrush landscapes in the Intermountain West (U.S.A.) for restoration. Restoration Ecology. 17: 652–659.

Meyer S.E.; Garvin, S.C.; Beckstead, J. 2001. Factors mediating cheatgrass invasion of intact salt desert shrubland. In: McArthur, D.E.; Fairbanks, D.J., comps. Shrubland ecosystem genetics and biodiversity: proceedings. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 224–232.

Miller, R.F.; Eddleman, L.L. 2001. Spatial and temporal Changes of sage grouse habitat in the sagebrush biome. Tech. Bull. 151. Corvallis, OR: Oregon State University, Agricultural Experiment Station. 35 p.

[illegible] treatments in sagebrush and pinyon-juniper ecosystems in the Great Basin: Evaluating resilience to disturbance and resistance to invasive annual grasses and predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-322-rev. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 68 p.

[illegible] Basin: Evaluating resilience to disturbance and resistance to invasive annual grasses and

predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-338. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 75 p.

(U"jNgaSZCOjNPsrc8IjewjoZ"3eNjqUj74GNjjGGjE6P4VqjRj6Z6U4V
and soils in the Great Basin Region: Response and ecological site characteristics. Gen. Tech. Rep. RMRS-GTR-308. Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Research Station. 126 p.

Miller R.F.; Knick, S.T.; Pyke, D.A.; [et al.]. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 145–185.

Monsen, S.B. 2005. Restoration manual for Colorado sagebrush and associated shrubland communities. Denver, CO: Colorado Division of Wildlife.

Monsen, S.B.; Stevens, R.; Shaw, N.L., eds. 2004. Restoring western ranges and wildlands. Gen. Tech. Rep. RMRS-GTR-136-vol-1. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 121–154.

Moynahan, B.J.; Lindberg, M.S.; Thomas, J.W. 2006. Factors contributing to process variance in annual survival of female Greater Sage-Grouse in Montana. Ecological Applications. 16: 1529–1538.

Naugle, D.E.; Doherty, K.E.; Walker, B.L.; [et al.]. 2011. Energy development and Greater Sage-Grouse. In: Knick S.T., Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 489–504.

Nielson, S.E.; Aldridge, C.L.; Hanser, S.E.; [et al.]. 2011. Occurrence of non-native invasive plants: The role of anthropogenic features. In: Hanser, S.E.; Leu, M.; Knick, S.T.; [et al.], eds. Sagebrush ecosystem conservation and management: Ecoregional assessment tools and models for the Wyoming Basins. Lawrence, KS: Allen Press: 357–377.

Noss, R.F.; LaRoe, E.T., III; Scott, J.M., 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Report 28. Washington, DC, National Biological Service.

Opdam, P.; Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation. 117: 285–297.

)NjR4VjSZN6CjV64Ga4NjP6N8qjP67UxjZU"xNjNUPIZPPjPPCjV6aUVZ"
report. Salem, OR: Oregon Department of Forestry. 105 p. http://www.odf.state.or.us/gis/data/Fire/West_Wide_Assessment/WWA_FinalReport.pdf [Accessed 17 June 2014].

)8"jN(ErZVEj+spHNVSZCfpNZHVm6VHjVEj4GESZVRjPUVPZRjONHPS
on Gunnison sage-grouse in Southwestern Colorado. Southwestern Naturalist. 46: 323–331.

cZNCjPZVrj4SjyeR"4OZ""8E4SjNjV6VRjN5NUV64GE"UCZ6jESZVRjUC5ZE6P
across natural systems. Nature. 421: 37–42.

Paruelo, J.M.; Lauenroth, W. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. Ecological Applications. 6: 1212–1224.

Pyke, D.A. 2011. Restoring and rehabilitating sagebrush habitats. In: Knick, S.T., Connelly, J. W., eds. Greater Sage-Grouse: Ecology and conservation of a landscape species and

its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 531–548.

Pyke, D.A.; Chambers, J.C.; Pellant, M.; [et al.]. 2015a. Restoration handbook for sagebrush steppe ecosystems with emphasis on Greater Sage-Grouse habitat—Part 1. Concepts for understanding and applying restoration: U.S. Geological Survey Circular 1416, 44 p., http://dx.doi.org/10.3133/cir1416.

Pyke, D.A.; Knick, S.T.; Chambers, J.C.; [et al.]. 2015b. Restoration handbook for sagebrush steppe ecosystems with emphasis on Greater Sage-Grouse habitat—Part 2. Landscape level restoration decisions. Circular 1418. U.S. Department of the Interior, U.S. Geological Survey. 21 p. http://dx.doi.org/10.3133/cir1418.

Redford, K.H.; Amoto, G., Baillie, J.; [et al.]. 2011. What does it mean to successfully conserve a (vertebrate) species? Bioscience. 61: 39–48.

Reever-Morghan, K.J.; Sheley, R.L.; Svejcar, T.J. 2006. Successful adaptive management: The integration of research and management. Rangeland Ecology and Management. 59: 216–219.

Rehfeldt, G.E.; Crookston, N.L.; Enz-Romero, C.M.; [et al.]. 2012. North American vegetation model for land-use planning in a changing climate: A solution to large E”ZPPUEZ6U4V5N4O”jCPmE4l”4RUEZ”e55”UEZ6U4VPL

Rehfeldt, G.E.; Crookston, N.L.; Warwell, M.; [et al.]. 2006. Empirical analyses of plant-climate relationships for the western United States. Journal of Plant Science. 167: 1123–1150.

Reisner, M.D.; Doescher, P.S.; Pyke, D.A. 2015. Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America’s semi-arid *Artemisia tridentata wyomingensis* ecosystems. Journal of Vegetation Science. doi: 10.1111/jvs.12327.

Reisner, M.D.; Grace, J.B.; Pyke, D.A.; [et al.]. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology. 50: 1039–1049.

Rinehart, S.M.; Zimmerman, A.F. 2001. The Bullseye Study: A quantitative and qualitative assessment of vegetation community characteristics observed as a function of distance from water on the Little Missouri National Grassland, western North Dakota. Missoula, MT: U.S. Department of Agriculture, Forest Service, Region 1. 33 p.

Rogers, G.E. 1964. Sage grouse investigations in Colorado. Tech. Publ. 16. Denver, CO: Colorado Game, Fish, and Parks Department.

Romme, W.H.; Allen, C.D.; Bailey, J.D.; [et al.]. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. Rangeland Ecology and Management. 62: 203–222.

Root, T.L.; Price, J.T.; Hall, K.R.; [et al.]. 2003. Fingerprints of global warming on wild animals and plants. Nature. 421: 57–60.

Roundy, B.A.; Young, K.; Cline, N.; [et al.]. 2014. Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangeland Ecology and Management. 67: 495–505.

Rowland, M.M.; Vojta, C.D., tech. eds. 2013. A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-GTR-89. Washington, DC: U.S. Department of Agriculture, a4NjP6+jNqUEjvZPSUVR64VjGEj5

Rowland, M.M.; Wisdom, M.J. 2009. Habitat networks for terrestrial wildlife: Concepts and case studies. Millspaugh, J.J., Thompson, F.R., III eds. Models for planning wildlife conservation in large landscapes. New York, NY: Elsevier: 501–531.

Rowland, M.M.; Kujawa, G.; Rickel, B.; [et al.]. 2013. Overview. Chapter 1. In: Rowland, M. M.; Vojta, C.D., tech. eds. 2013. A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-GTR-89. Washington, DC: U.S. Department of Agriculture, Forest -jNqUEjvZPSUVR64VjGEj5

Rowland, M.M.; Wisdom, M.J.; Suring, L.H.; [et al.]. 2006. Greater Sage-Grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation. 129: 323–35

Sage Grouse Initiative [SGI]. 2015. Reducing cultivation of grazing lands conserves sage grouse. Science to Solutions Series Number 8. Sage Grouse Initiative. 4 p. http://www.sagegrouseinitiative.com/.

Sala, O.E.; Lauenroth,W.K.; Gollucio, R.A. 1997. Plant functional types in temperate semi-arid regions. In: Smith, T.M.; Shugart, H.H.; Woodward, F.I., eds. Plant functional types. Cambridge, UK: Cambridge University Press: 217–233.

Salo, L.F. 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: Possible modes for early introductions, subsequent spread. Biological Invasions. 7: 165–180.

Saunders, D.A.; Hobbs, R.J.; Margules, C.R. 1991. Biological consequences of fragmentation: A review. Conservation Biology 5: 18–32.

Schlaepfer, D.R.; Lauenroth, W.K.; Bradford, J.B. 2012. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. Ecography. 35: 374–384.

Schrag, A.; Konrad, S.; Miller, S.; Walker, B.; Forrest, S. 2010. Climate-change impacts on sagebrush habitat and West Nile virus transmission risk and conservation implications for Greater Sage-Grouse. GeoJournal. doi 10.1007/s10708-010-9369-3.

Schroeder, M.A.; Vander Haegen, M. 2011. Response of Greater Sage-Grouse to the Conservation Reserve Program in Washington State. In: Knick S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 517–530.

Scott, J.M.; Goble, D.D.; Haines, A.M.; Wiens, J.A.; Neel, M.C. 2010. Conservation-reliant species and the future of conservation. Conservation Letters. 3: 91–97.

Seager, R.; Ting, M.; Held, I.; [et al]. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science. 316: 1181–1184.

-SUVVjCZMspZIjNvtUP64NUEZ”NjZMxCH”6UxjEZxZ”xN4HRS6ZPE4V6j/6G4N piñon-juniper woodland restoration in Western Colorado. Ecological Applications. 19: 1231—1245.

Smith, J.T.; Evans, J.S.; Baruch-Mordo, S.; [et al.]. 2016. Reducing cropland conversion risk to sage-grouse through strategic conservation of working rangelands. Biological Conservation. 201: 10–19.

Smith, J.T.; Flake, L.D.; Higgins, K.F.; [et al.]. 2005. Evaluating lek occupancy of Greater Sage-Grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist. 65: 310–320.

Smith, K.T.; Kirol, C.P.; Beck, J.L.; [et al.]. 2014. Prioritizing winter habitat quality for [illegible] 5(2):15. http://dx.doi.org/10.1890/ES13-00238.1.

Smith, S.D.; Nowak, R S. 1990. Ecophysiology of plants in the Intermountain lowlands. In: Osmond, C.B.; Pitelka, L.F.; Hidy, G.M., eds. Plant Biology of the Basin and Range. Springer-Verlag: 179–242.

Soil Survey Staff. 2014a. Soil Survey Geographic (SSURGO) Database. U.S. Department of Agriculture, Natural Resources Conservation Service. http://sdmdataaccess.nrcs.usda.gov/ [Accessed June 13, 2016].

Soil Survey Staff. 2014b. U.S. General Soil Map (STATSGO2) Database. United States Department of Agriculture, Natural Resources Conservation Service. http://sdmdataaccess.nrcs.usda.gov/ [Accessed June 13, 2016].

Stanley, T.R.; Aldridge, C.L.; Saher, D.J.; [et al.]. 2015. Daily nest survival rates of Gunnison Sage-Grouse (*Centrocercus minimus*): Assessing local- and landscape-scale drivers. The Wilson Journal of Ornithology. 127: 59–71.

Stevens, B.S.; Connelly, J.W.; Reese, K.P. 2012. Multi-scale assessment of Greater Sage-Grouse fence collision as a function of site and broad scale factors. Journal of Wildlife Management. 76 (7): 1370–1380.

Still, S.M.; Richardson, B.A. 2015. Projections of contemporary and future climate niche for Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*): A guide for restoration. Natural Areas Journal. 35: 30–43.

Stiver, S.J.; Apa, A.D.; Bohne, J.R.; [et al.]. 2006. Greater Sage-grouse comprehensive [illegible] Wildlife Agencies, Cheyenne, WY.

Stohlgren, T.J.; Owen, A.J.; Lee, M. 2000. Monitoring shifts in plant diversity in response to climate change: A method for landscapes. Biodiversity and Conservation. 9: 165–186.

Stringham, T.K.; Krueger, W.C.; Shaver, P.L. 2003. State and transition modeling: An ecological process approach. Journal of Range Management. 56: 106–113.

Suring, L.H.; Rowland, M.M.; Wisdom, M.J. 2005. Identifying species of conservation concern. In: Wisdom, M.J.; Rowland, M.M.; Suring, L.H., eds. Habitat threats in the sagebrush ecosystem: Methods of regional assessment and applications in the Great Basin. Lawrence, KS: Alliance Communications Group: 50–162.

Swanson, C.C.; Rumble, M.A.; Grovenburg, T.W.; [et al.]. 2013. Greater Sage-Grouse winter habitat use on the eastern edge of their range. Journal of Wildlife Management. 77: 486–494.

Tack, J.D.; Naugle, D.E.; Carlson, J.C.; [et al.]. 2012. Greater Sage-Grouse *Centrocercus urophasianus* migration links the USA and Canada: A biological basis for international prairie conservation. Oryx. 46: 64.

Taylor, K.; Brummer, T.J.; Lavin, M.; [et al.]. 2014. *Bromus tectorum* [illegible] with climate conditions. Ecosystems. 17: 960–973.

Taylor R.L.; Tack, J.D.; Naugle, D.E.; [et al.]. 2013. Combined effects of energy development and disease on Greater Sage-Grouse. PLoS ONE 8(8): e71256.

Thomson, A.M.; Crowe, K.A.; Parker, W.H. 2010. Optimal white spruce breeding zones for Ontario under current and future climates. Canadian Journal of Forest Research. 40: 1576–1587.

Thompson, K.M.; Holloran, M.J.; Slater, S.J.; [et al.]. 2006. Early brood-rearing habitat use and productivity of Greater Sage-Grouse in Wyoming. Western North American Naturalist. 66: 332–342.

Travis, J.M.J. 2003. Climate change and habitat destruction: A deadly anthropogenic cocktail. Proceedings of the Royal Society of London Series B-Biological Sciences. 270: 467–473.

nCOZVS47ZNmsNgjEjV6NjSUP64N84G6Sj14N6SjNVyNjZ6c”ZUVPeCjNUEZV□ Midland Naturalist. 135: 115–121.

USDA Natural Resources Conservation Service [USDA NRCS]. 2016. National cooperative soil survey. Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service. http://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/partnership/ncss/ [Accessed Sept. 1, 2016].

USDA Natural Resources Conservation Service [USDA NRCS]. 2015a. Ecological site descriptions. Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service. http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/ [Accessed June 13, 2016].

USDA Natural Resources Conservation Service [USDA NRCS]. 2015b. Sage grouse initiative. Wildlife conservation through sustainable ranching. Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service. http://www.sagegrouseinitiative.com. [Accessed June 13, 2016].

n+ljSZN6CjV64G6SjoV6jNU4Nwn+io3ZeVUV6jRNZ6jxNZVRj”ZVxNjCZVZRjCjV6□ strategy. Final Report to the Secretary of the Interior. https://www.forestsandrangelands.gov/rangeland/documents/IntegratedRangelandFireManagementStrategy_FinalReportMay2015.pdf. [Accessed June 25, 2016].

U.S. Department of the Interior [USDI]. 2015b. gZVRj”ZVxNj5NjqjV6U4VCZVZRjCjV6□ and restoration. Secretarial Order Number 3336. http://www.forestsandrangelands.gov/rangeland/documents/SecretarialOrder3336.pdf. [Accessed June 13, 2016].

U.S. Department of the Interior [USDI]. 2016. Safeguarding America’s lands and waters from invasive species: A national framework for early detection and rapid response, Washington, DC: U.S. Department of the Interior. 55 p. https://www.doi.gov/sites/doi.R4q”jP1Z6U4VZ”migaNZCj74NI5xG . [Accessed July 17, 2016]

USDI Bureau of Land Management [USDI BLM]. 2012. Burned areas emergency stabilization and rehabilitation handbook (public). BLM Handbook H-1742-1. Washington, DC: U.S. Department of the Interior, Bureau of Land Management. 80 p. http://www.blm.gov/style/medialib/blm/wo/Information_Resources_Management/policy/blm_handbook.Par.52739.File.dat/h1742-1.pdf [Accessed June 13, 2016].

USDI Bureau of Land Management [USDI BLM]. 2009. Consolidated response to 2009 Gunnison sage-grouse status review information request outline from the Colorado State)GEjyHVVUP4VaUj”x)GEjnVE4C5ZSRNjaUj”x)GEji4”4NjPc HO”UEtZVxP)GEj□

Interior, Bureau of Land Management. 100 p.

Invasive Annual Grasses, and Conifer Expansion Assessment. Washington, DC: U.S. Department of the Interior, Bureau of Land Management. http://www.nifc.gov/ [Accessed Aug. 3, 2016].

U.S. Fish and Wildlife Service [USFWS]. 2010. Endangered and threatened wildlife and *Centrocercus urophasianus*) as threatened or endangered; proposed rule. Fed. Register 75, 13910–14014. http://www.fws.gov/policy/library/2010/2010-5132.pdf [Accessed June 13, 2016].

U.S. Fish and Wildlife Service [USFWS]. 2013. Greater Sage-Grouse (*Centrocercus urophasianus*) Conservation Objectives: Final Report. Denver, CO: U.S. Department of the Interior, U.S. Fish and Wildlife Service. 91 p.

U.S. Fish and Wildlife Service [USFWS]. 2014a. Endangered and threatened wildlife and 69310. https://www.federalregister.gov/articles/2014/11/20/2014-27109/endangered-and-threatened-wildlife-and-plants-threatened-status-for-gunnison-sage-grouse [Accessed June 13, 2016].

U.S. Fish and Wildlife Service [USFWS]. 2014b. Endangered and threatened rule. Fed. Register 79 No. 224, 69312–69363. https://www.federalregister.gov/articles/2014/11/20/2014-27113/endangered-and-threatened-wildlife-and-plants-designation-of-critical-habitat-for-gunnison [Accessed June 13, 2016].

U.S. Fish and Wildlife Service [USFWS]. 2015. Endangered and threatened wildlife and *Centrocercus urophasianus*) as an endangered or threatened species; proposed rule. Fed. Register 80, 59858–59942. http://www.gpo.gov/fdsys/pkg/FR-2015-10-02/pdf/2015-24292.pdf. [Accessed June 13, 2016].

U.S. Geological Survey [USGS]. 2015. Land treatment digital library. Reston, VA: U.S. Department of the Interior, U.S. Geological Survey. http://ltdl.wr.usgs.gov/ [Accessed June 13, 2016].

U.S. Geological Survey [USGS]. 2013: LANDFIRE 1.2.0 Existing Vegetation Type layer. Updated 3/13/2013. Reston, VA: U.S. Department of the Interior, U.S. Geological Survey. [Accessed June 13, 2016].

occupied and vacant-unknown habitat. Last updated March 2012. Salt Lake City, UT: State of Utah, Division of Wildlife Resources. http://dwrcdc.nr.utah.gov/ucdc/downloadgis/disclaim.htm [Accessed June 13, 2016].

Vander Haegen, W.M.; Dobler, F.C.; Pierce, D.J. 2000. Shrub steppe bird response to habitat and landscape variables in eastern Washington, USA. Conservation Biology. 14: 1145–1160.

Veblen, K.E.; Pyke, D.A.; Aldridge, C.L.; [et al.]. 2011. Range-wide assessment of livestock grazing across the sagebrush biome. Open-File Report 2011–1263. Reston, VA: U.S. Department of the Interior, U.S. Geological Survey.

Vojta, C.D.; McDonald, L.L.; Brewer C.K.; [et al.]. 2013. Chapter 3: Planning and design for habitat monitoring. In: Rowland, M. M.; Vojta, C.D., tech. eds. 2013. A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-GTR-89. Washington, DC:

Walker, B.L.; Apa, A.D.; Eichhoff, K. 2016. Mapping and prioritizing seasonal habitats for Greater Sage-Grouse in Northwestern Colorado. Journal of Wildlife Management. 80: 63–76.

Walker, B.L.; Naugle, D.E.; Doherty K.E. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management. 71: 2644–2654.

West, N. E. 1983a. Great Basin-Colorado Plateau sagebrush semi-desert. In: West, N.E., ed. Temperate deserts and semi-deserts. Amsterdam, The Netherlands: Elsevier Publishing Company: 331–350.

West, N.E. 1983b. Intermountain salt-desert shrubland. In: West, N.E., ed. Temperate deserts and semi-deserts. Amsterdam, The Netherlands: Elsevier Publishing Company: 375–378.

Western Governors Association. 2015. Sage grouse inventory: 2014 conservation initiatives. Special Report by Western Governors. http://www.westgov.org/images/dmdocuments/2014_WGA_Sage_Grouse_Inventory_Final_lo_res.pdf [Accessed June 13, 2016].

Willard, E.E.; Bedunah, D.J.; Marcum, C.L.; [et al.]. 1988. Environmental factors affecting spotted knapweed. Biennial Report 1987–1988. Missoula, MT: University of Montana, School of Forestry, Montana Forest and Conservation Experiment Station. 21 p.

Williams M.I.; Dumroese R.K. 2013. Preparing for climate change: Forestry and assisted migration. Journal of Forestry. 111: 287–297.

Winward, A.H. 2004. Sagebrush of Colorado: Taxonomy, distribution, ecology, and management. Denver, CO: Colorado Division of Wildlife. 41 p.

Wisdom, M.J.; Chambers, J.C. 2009. A landscape approach for ecologically-based management of Great Basin shrublands. Restoration Ecology. 17: 740–749.

Wisdom, M.J.; Meinke, C.W.; Knick, S.T.; [et al.]. 2011. Factors associated with extirpation of sage-grouse. In: Knick, S.T.; Connelly, J.W., eds. Greater Sage-Grouse—Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. Berkeley, CA: University of California Press: 451–474.

Wisdom, M.J.; Rowland, M.M.; Suring, L.H., eds. 2005. Habitat threats in the sagebrush ecosystem: Methods of regional assessment and applications in the Great Basin. Lawrence, KS: Allen Press. 301 p.

Xian, G.; Homer, C.G.; Aldridge, C.L. 2011 Effects of land cover and regional climate variations on long-term spatiotemporal changes in sagebrush ecosystems. GIScience & Remote Sensing. 49: 378–396.

Young, K.R.; Roundy, B.A.; Eggett, D.L. 2013. Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. Forest Ecology and Management. 310: 777–785.

At-Risk Community Phase — A community phase that can be designated within the reference state and also in alternative states. This community phase is the most vulnerable to transition to an alternative state (Caudle et al. 2013).

Community Phase — A unique assemblage of plants and associated soil properties that can occur within a state (Caudle et al. 2013).

Ecological Site (ES) — A conceptual division of the landscape that is defined as a distinctive kind of land based on recurring soil, landform, geological, and climate characteristics that differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation and in its ability to respond similarly to management actions and natural disturbances (Caudle et al. 2013).

Ecological Site Descriptions (ESD) — The documentation of the characteristics of an ecological site. The documentation includes the data used to define the distinctive properties and characteristics of the ecological site, the biotic and abiotic characteristics that differentiate the site (i.e., climate, physiographic, soil characteristics, plant communities), and the ecological dynamics of the site that describes how changes in disturbance processes and management can affect the site. An ESD also provides interpretations about the land uses and ecosystem services that a particular ecological site can support and management alternatives for achieving land management (Caudle et al. 2013).

Ecological Type — A category of land with a distinctive (i.e., mappable) combination of landscape elements. The elements making up an ecological type are climate, geology, geomorphology, soils, and potential natural vegetation. Ecological types differ from each other in their ability to produce vegetation and respond to management and natural disturbances (Caudle et al. 2013).

Major Land Resource Area — A geographic area, usually several thousand acres in extent, that is characterized by a particular pattern of soils, climate, water resources, land uses, and type of agriculture.

Resilience — Ability of a species and/or its habitat to recover from stresses and disturbances. Resilient ecosystems reorganize and regain their fundamental structure, processes, and functioning when altered by stresses like increased CO_2, nitrogen deposition, and drought and to disturbances like land development and fire (Holling 1973).

Resistance — Capacity of an ecosystem to retain its fundamental structure, processes, and functioning (or remain largely unchanged) despite stresses, disturbances, or invasive species (Folke et al. 2004).

Resistance to Invasion — Abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen 2004).

Restoration Pathways — Restoration pathways describe the environmental conditions and practices that are required to recover a state that has undergone a transition (Caudle et al. 2013).

State — A suite of community phases and their inherent soil properties that interact with the abiotic and biotic environment to produce persistent functional and

structural attributes associated with a characteristic range of variability (adapted from Briske et al. 2008).

State-and-Transition Model —A method to organize and communicate complex information about the relationships between vegetation, soil, animals, hydrology, disturbances (fire, lack of fire, grazing and browsing, drought, unusually wet periods, insects and disease), and management actions on an ecological site (Caudle et al. 2013).

Thresholds — Conditions sufficient to modify ecosystem structure and function beyond the limits of ecological resilience, resulting in transition to alternative states (Briske et al. 2008).

Transition — Transitions describe the biotic or abiotic variables or events, acting independently or in combination, that contribute directly to loss of state resilience and result in shifts between states. Transitions are often triggered by disturbances, including natural events (climatic events or fire) and/or management actions (grazing, burning, fire suppression). They can occur quickly as in the case of catastrophic events like fire or flood, or over a long period of time as in the case of a gradual shift in climate patterns or repeated stresses like frequent fires (Caudle et al. 2013).

Moisture Regime Data

Soil climate regimes (temperature and moisture) are used in soil taxonomy to classify soils. They are important to consider in land management decisions because bance and management actions. Soil temperature and moisture regimes are assigned to soil map unit components as part of the National Cooperative Soil Survey pro- classes are listed below. Complete descriptions can be found in the 12th edition of the *Keys to Soil Taxonomy* (http://www.nrcs.usda.gov/wps/PA_NRCSConsumption/download?cid=stelprdb1252094&ext=pdf).

Exhibit A2.1. the Eastern Range

Soil Temperature Regimes

Cryic (cold): Soils that have a mean annual soil temperature between 0 and 8 °C and do not have permafrost, at a depth of 50 cm below the surface or at a restrictive feature, whichever is shallower.

Frigid (cool): Soils that have a mean annual soil temperature between 0 and 8 °C and the difference between mean summer and mean winter soil temperatures is >6 °C at a depth of 50 cm below the surface or at a restrictive feature, whichever is shallower.

Mesic (warm): Soils that have a mean annual soil temperature of 8–15 °C and the difference between mean summer and mean winter soil temperatures is >6 °C at a depth of 50 cm below the surface or at a restrictive feature, whichever is shallower.

Soil Moisture Regimes

Udic (moist): Characteristic of high elevation areas with winter snowfall and/or summer precipitation. The soil is dry for less than 90 consecutive days in normal years.

Ustic (summer moist): Generally there is some plant-available moisture during precipitation allows presence of warm season plant species. The soil is dry for 90 or more cumulative days in normal years.

Xeric (winter moist; generally mapped at >12 inches mean annual precipitation): Characteristic of areas where winters are moist and cool and summers are warm and dry. The soil is dry for 45 or more consecutive days in the 4 months following the summer solstice but moist in some part for 90 or more consecutive days during the growing season.

Aridic (dry; generally mapped at <12 inches mean annual precipitation): Characteristic of arid regions. The soil is dry for at least half the growing season and moist for less than 90 consecutive days.

Soil moisture regimes are further divided into moisture subclasses, which are often used to indicate soils that are transitional between moisture regimes. For example, a soil with an aridic moisture regime and a xeric moisture subclass may be described as "Aridic bordering on Xeric." Understanding these gradients becomes increasingly important when making interpretations and decisions at the project scale where aspect, slope, and soils affect the actual moisture regime. More information on taxonomic moisture subclasses is available at http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/ref/?cid=nrcs142p2_053576.

We used soil survey spatial and tabular data aggregated in October 2013 to facilitate broad scale analyses of resilience and resistance across the eastern range of sage-grouse (Maestas et al. 2016). Soils data were derived from two primary sources: (1) completed and interim soil surveys available through the Soil Survey Geographic Database (SSURGO) (Soil Survey Staff a), and (2) the State Soils Geographic Database (STATSGO2) (Soil Survey Staff b). Data for the eastern range 7jNjH5xZ6jxUVsZVHZN864NjjE66SjC4P6EHNNjV6P4U"BHNqj8UVG4NCZ6U4V ZqZU"ZO"jR6VP4CjEZPjPZONH56ESZVRjPUVP4U"6jC5jZ6HNjZVxC4UP6HNj regimes are apparent when merging together STATSGO2 and SSURGO soil survey areas due to differences in data collection and publication, scale of interpretation, or changes in application of regime concepts. The area near the border between southeastern Montana and northeastern Wyoming is in a transition zone between the frigid and mesic soil temperature regimes, which has resulted in an apparent abrupt change in temperature regime at the State border. Future updates to soil survey information will resolve these join issues along political boundaries, using current E"UCZ6jxZ6ZPj6PZVxZxxU6U4VZ"j"xxZ6Z

We used soil temperature regime and moisture regime subclass data to gener-Z6jZPUC5"UjxUVxj/4GNj"Z6UqjNjPU"UjVEjZVxNjPUP6ZVZPj6jNVNZVRj6SZ6 has three categories: high, moderate, and low. We used the relationship among the predominant ecological types in the eastern range, soil temperature and moisture regimes, and relative resilience and resistance (table 3) to inform these categories. Because of the distinct climatic regimes and vegetation responses in the West-Central Semiarid Prairies in MZ I and Cold Deserts in MZ II and VII, the rankings for these ecoregions were performed separately. The Mesic/Ustic bordering on Aridic and Mesic/Aridic bordering on Ustic regimes were ranked as moderate in the West-Central Semiarid Prairies in MZ I and as low in the Cold Deserts in MZ II and VII. Soils with high water tables, wetlands, or frequent ponding or uncommon regimes that would not typically support sagebrush were excluded.

Soils geodatabases and categorized resilience and resistance layers can be accessed at: https://www.sciencebase.gov/catalog/item/538e5aa9e4b09202b547e56c.

Exhibit A2.2. Resilience and resistance (R&R) rating for the soil temperature and moisture regimes.

Soil Taxonomic Name	Common Name	R&R Rating
Cryic/Udic-Typic	Cold and moist	High
Cryic/Ustic-Typic	Cold and summer moist	High
Frigid/Ustic-Typic	Cool and summer moist	High
Frigid/Xeric-Typic	Cool and winter moist	High
Frigid/Ustic bordering on Aridic	Cool and summer moist bordering on dry	Moderate
Frigid/Aridic bordering on Ustic	Cool and dry bordering on summer moist	Moderate
Frigid/Aridic-Typic	Cool and dry	Moderate
Mesic/Ustic-Typic	Warm and summer moist	Moderate
Mesic/Ustic bordering on Aridic	Warm and summer moist bordering on dry	Moderate (Prairies) Low (Cold Deserts)
Mesic/Aridic bordering on Ustic	Warm and dry bordering on summer moist	Moderate (Prairies) Low (Cold Deserts)
Mesic/Aridic-Typic	Warm and dry	Low

Ecological Types

The steps used to determine the ecological types that dominate the eastern range of Greater sage-grouse and the range of Gunnison sage-grouse are outlined below.

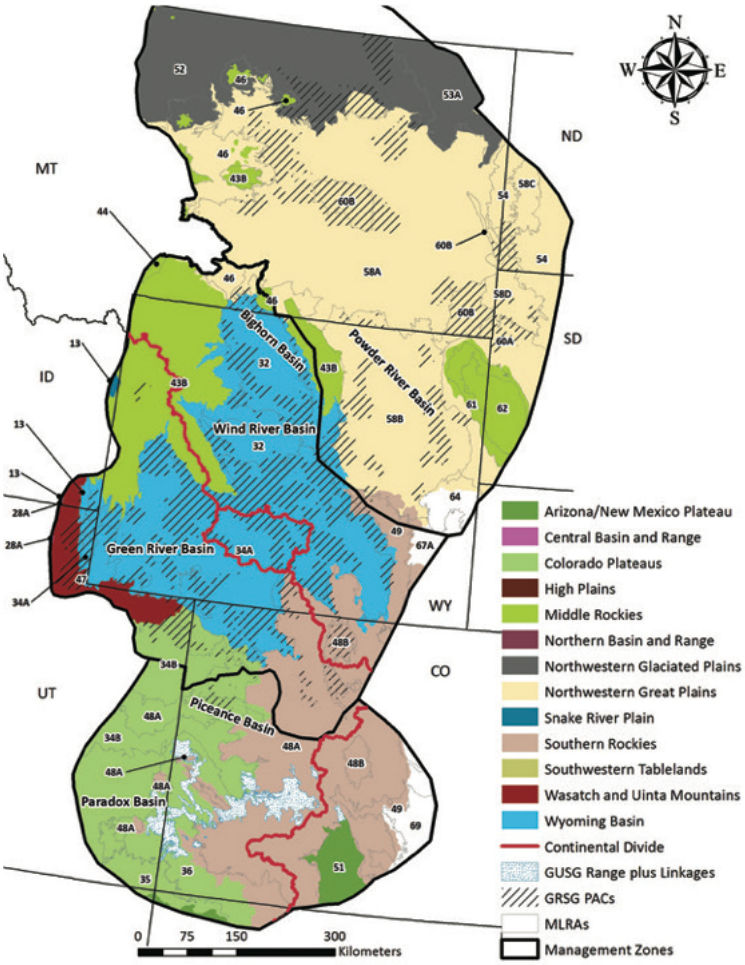
1. National Soil Information System (NASIS) data were exported for each Environmental Protection Agency Level II Ecoregion, including Cold Deserts (10.1), Western Cordillera (6.2), and West Central Semiarid Prairies (9.3), within the eastern range of Greater sage-grouse, (Management Zones I, II, and VII), and the range of Gunnison sage-grouse. The information exported included acreages of the dominant Ecological Site (ES) within the Greater sage-grouse Priority Areas of Conservation (PACs) and Gunnison sage-grouse critical habitat as well as soil temperature regime, moisture regime, and moisture subclass assigned at the soil map unit component level. The analyses were conducted by Steve Campbell, NRCS, Portland, Oregon.
2. Ecological Site Descriptions (ESDs) were first sorted by Major Land Resource Area (MLRA) and State and then by soil temperature regime, moisture regime, and moisture subclass to evaluate the ecological sites most often correlated with the PACs. A map was produced intersecting Level III Ecoregions with MLRAs and PACs (fig. A3.1). Each Level II Ecoregion spreadsheet was filtered by central MLRA concepts for the Ecoregion as follows:
    a. Cold Deserts MLRAs:

        32—Northern Desertic Basins: Bighorn and Wind River Basins [illegible] precipitation 5–12” (Aridic-Typic, Aridic bordering on Ustic, Ustic bordering on Aridic); and average annual temperature 4–9 °C (Frigid, Mesic)

        34A—Cool Central Desertic Basins and Plateaus: Wyoming [illegible] Ustic bordering on Aridic); and average annual temperature 5–7 °C (Frigid)

        34B—Warm Central Desertic Basins and Plateaus: Uinta Basin [illegible] on Ustic, Ustic bordering on Aridic); and average annual temperature 7–12 °C (Mesic)

        36—Southwestern Plateaus, Mesas, and Foothills: Canyonlands [illegible] Colorado/Utah in identified Gunnison sage-grouse areas; average precipitation 12–20” (Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic); and average annual temperature 7–14 °C (Mesic)



—Map of the Major Land Resource Areas (MLRAs) intersected with the Level III ecoregions, management zones, Greater sage-grouse Priority Areas for Conservation, and Gunnison sage-grouse range plus linkages (GSGRSC 2005; UDWR 2012; USFWS 2014a).

b. Western Cordillera MLRAs:

43B—Central Rocky Mountains: very large, covers Montana 5kZS4ZVxv84CUVRCH6Z55"UEZO"jZNjZPG4N□ this area mostly reside in Wyoming; average precipitation 25–60" (Udic); and average annual temperature <3 °C (Cryic)

46—Northern Rocky Mountain Foothills: conceptually occurs only in Montana, but concept has been proposed and accepted for use in Wyoming for foothills which are current grouped into 32, 34A, or 43B but do not fit MLRA concept; average precipitation 1–20" (Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic); and average annual temperature 1–9 °C (Cryic, Frigid, Mesic)

47—Wasatch and Uinta Mountains: [illegible] precipitation 16-30+" (Xeric-Typic, Xeric bordering on Ustic, Ustic bordering on Xeric, Ustic-Typic, Udic bordering on Ustic, Udic-Typic); and average annual temperature 1–7 °C (Cryic, Frigid)

48A—Southern Rocky Mountains: [illegible] Colorado and Wyoming and includes areas of importance to Gunnison sage-grouse as well as Greater sage-grouse; average precipitation 16–32 (50)" (Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic, Udic-Typic); and average annual temperature 3–9 °C (Cryic, Frigid, warm Frigid)

48B—South Rocky Mountain Parks: [illegible] Parks; average precipitation 10–16" (Ustic bordering on Aridic, Ustic-Typic); and average annual temperature 1–6 °C (Cryic, Frigid)

c. West-Central Semiarid Prairies MLRAs:

52—Brown Glaciated Plain: northern Montana above Hwy 2; average precipitation 10–17" (Ustic bordering on Aridic, Ustic-Typic); and average annual temperature 4–7 °C (Frigid)

54—Rolling Soft Shale Plain: [illegible] tion 14–18" (Ustic bordering on Aridic, Ustic-Typic); and average annual temperature 3–8 °C (Frigid)

58A—Northern Rolling High Plains, Northern Part: mostly [illegible] precipitation 8–22" (Aridic bordering on Ustic, Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic); and average annual temperature 5–10 °C (Frigid, Mesic)

58B—Northern Rolling High Plains, Southern Part: mostly [illegible] precipitation 9–27" (Aridic bordering on Ustic, Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic, Udic-Typic); and average annual temperature 5–9 °C (Frigid, Mesic)

58C—Northern Rolling High Plains, Northeastern Part: mostly [illegible] precipitation 14–17" (Ustic bordering on Aridic, Ustic-Typic); and average annual temperature 5–7 °C (Frigid)

58D—Northern Rolling High Plains, Eastern Part: mostly South [illegible] Ustic-Typic); and average annual temperature 6–7 °C (Frigid)

60A—Pierre Shale Plains: [illegible] cable areas for this analysis reside mostly in South Dakota; average precipitation 13–22" (Ustic bordering on Aridic, Ustic-Typic, Udic bordering on Ustic, Udic-Typic); and average annual temperature 6–9 °C (Frigid, Mesic)

60B—Pierre Shale Plains, Northern Part: mostly in Montana [illegible] erage precipitation 1–15" (Ustic bordering on Aridic); and average annual temperature 6–8 °C (Frigid)

3. The Ecological Site Information System (ESIS) was used to query dominant ESDs supporting big sagebrush plant communities based on NASIS export, MLRA concept, and consultation with NRCS State Rangeland Management Specialists or equivalent. In some cases, ES concepts exist with no STM and/or there are variable STM concepts depending on age of ESDs. The most contemporary STMs were prioritized for consideration, but older products were used when they were the best available product to represent a regime concept. Individuals consulted were:
    a. Kirt Walstead, Jon Siddoway, Tammy Decock, Montana
    b. Rachel Murph and Suzanne Mayne, Colorado
    c. Shane Green, Dean Stacy, Utah
    d. Jeff Prince, Jody Forman, North Dakota
    e. Stan Boltz, South Dakota
    f. Karen Clause, Ray Gullion, Jim Haverkamp, George Gamblin, Ryan Murray, Marji Patz, and Bryan Christensen, Wyoming
    g. Brendan Brazee, Idaho
4. Potentially representative ESs were downloaded to folders and organized by soil temperature/moisture regime concepts. Often the various resources used were not in agreement, and each area was reviewed to determine the best source of data. Resources used to determine the regime include:
    a. ESD climate section
    b. LRU concept or state ecological zones, when available
    c. MLRA Description climate section—edits to MLRA descriptions are anticipated by local staff providing input on these descriptions, and have been incorporated as appropriate
    d. NASIS assigned temperature and moisture regime by mapunit component and accompanying map—many areas in this region are populated with older mapping concepts or are not populated in NASIS
    e. PRISM maps
5. Regime concepts with representative MLRAs and ESDs listed here for reference:
    a. Cold Deserts
        i. Frigid bordering on Cryic/Ustic bordering on Aridic (Cool bordering on Cold, Summer Moist bordering on Dry)

        Representative Area: Wyoming Basin—MLRA 34A in Wyoming west of continental divide into Rich County, Utah; Note: More applicable to Dillon Area than the Great Basin as described in Chambers et al. (2014a).

Status of ESDs: Wyoming has draft Land Resource Unit concepts developed and a couple of contemporary STMs in Wyoming plus older vintage examples

1. R034AC122WY_LoamyPP_Provisional2014cold
2. R034AC150WY_SandyPP_Provisional2014cold
3. R034AY222WY_Loamy10-14W_Provisional2005
4. R034AY250WY_Sandy10-14W_Provisional2005

ii. Frigid/Ustic bordering on Aridic (Cool, Summer Moist bordering on Dry)

Representative Area: Wyoming Basin—MLRA 34A in Wyoming's lower Green River Basin (west of continental divide) and Great Divide Basin

Status of ESDs: In Wyoming, 1 contemporary draft STM and older vintage sites; in Utah a contemporary draft STM

1. R034AF122WY_LoamyBR_DRAFT2015
2. R034AI122WY_LoamyPV_DRAFT2015warm
3. R034AY322WY_Loamy10-14SE_Provisional2005
4. R034AY350WY_Sandy10-14SE_Provisional2005
5. R046XA122WY_Loamy10-14E-Frigid_DRAFT-ALL

iii. Frigid/Aridic bordering on Ustic (Cool, Dry bordering on Summer Moist)

Representative Area: Wyoming Basin—MLRA 34A in Green River Basin (west of continental divide) and Great Divide Basin

Status of ESDs: In Wyoming, 1 contemporary draft STM and older vintage sites plus into Utah a contemporary draft STM

1. R034AB122WY_LoamyGR_DRAFT2015
2. R034AY122WY_LoamyGR_Provisional2005
3. R034AY150WY_SandyGR_Provisional2005
4. R034AY220UT_Semi-desertLoam_DRAFT

iv. Mesic/Ustic bordering on Aridic (Warm, Summer Moist bordering on Dry)

Representative Area: Wyoming Basin—MLRA 32 foothills in Wyoming, MLRA 34B and 36 in Colorado and Utah; potential Gunnison sage-grouse; Potential for juniper or pinyon-juniper invasion. This is 10-14" ppt in Wyoming, but 12 to 16" ppt in Colorado, Utah, and New Mexico

Status of ESDs: Contemporary vintage STMs in Colorado and Wyoming

1. R032XD122WY_Loamy10-14BH_Provisional2014
2. R034AY289CO_ClayeyFoothhills_DRAFT- – is really a 36 site –miss labeled in NASIS
3. R036XY284CO – Loamy Foothills
4. R036XY306UT_UplandLoam_2008Prov

v. Mesic/Aridic-Typic (Warm, Dry)

Representative Area: Wyoming Basin—LRA 32 in Wyoming (Bighorn and Wind River Basins) ONLY

Status of ESDs: 1 contemporary STM and older examples of STMs included; Utah and Colorado sites in this zone are salt desert shrub sites and outside scope of analysis (no big sage)

1. R032XA122WY_Loamy5-9BH_Provisional2014
2. R032XY150WY_Sandy5-9BH_Provisional2005
3. R032XY222WY_Loamy5-9WR_Provisional2005
4. R032XY250WY_Sandy5-9WR_Provisional2005

vi. Mesic/Aridic bordering on Ustic (Warm, Dry bordering on Summer Moist)

Representative Area: Wyoming Basin and Colorado Plateau—MLRAs 32 foothills in Wyoming and MLRA 34B and 36 in Colorado and Utah; Gunnison sage-grouse potential in Colorado

Status of ESDs: Wyoming has a couple contemporary STMs and MLRA 34B in Utah and Colorado have some contemporary draft STMs

1. R032XY124WY_LoamyCalc10-14E_Provisional2014
2. R034A-BY327CO_SemidesertLoam_RangeSiteOnly
3. R034BY212UT_SemidesertLoam_DRAFT

vii. Frigid bordering on Mesic/Ustic-Typic (Cool bordering on Warm, Summer Moist)

Representative Area: Colorado Plateau—MLRA 48A/34A Piceance Basin-Book Cliffs in Colorado/Utah (This zone is treated as 48A, but some 34A shows on map); Gunnsion sage-grouse potential

Status of ESDs: Colorado has a draft contemporary STM

1. R034AY285CO_FoothillSwale_DRAFT2014

b. Western Cordillera

i. Cryic/Ustic-Typic (Cold, Summer Moist)

Representative Area: Middle and Southern Rockies – MLRAs 46/43B Foothills in Wyoming & Montana; MLRA 48A in Wyoming and Northern Colorado (north of Colorado River/I-70); MLRA 49 in Wyoming (not in Colorado); potential Gunnison sage-grouse in Colorado

Status of ESDs: MLRA 43B has contemporary draft STM from Idaho and older vintage from Wyoming; MLRA 49 has older vintage STM from Wyoming; MLRA 48 DRAFT site in Wyoming

1. R043BY009ID_Loamy 16-20_DRAFT
2. R043BY222WY_Loamy15-19W_Provisional2007
3. R043BY322WY_Loamy15-19E_Provisional2007
4. R048AY122WY_Loamy15-19SE_DRAFT
5. R049XA122WY_Loamy15-19SE_Provisional2008

ii. Cryic/Udic (Cold, Wet)

Representative Area: Middle and Southern Rockies—MLRA 43B in Wyoming and Montana; areas of 48A in Colorado; MLRA 47 (Wasatch north and south) high mountain valleys; potential Gunnison sage-grouse in Colorado

Status of ESDs: MLRA 43B has contemporary draft STM from Idaho and older vintage from Wyoming; MLRA 47 has contemporary STM from Utah and DRAFT site in 48A in Colorado

1. R043BY003ID_Loamy 22+_DRAFT
2. R043BY122WY_Loamy20M_Provisional2007
3. R047XA516UT_HighMtnLoam_Provisional2012
4. R048AY250CO_SubalpineLoam_2015DRAFT

iii. Frigid/Ustic-Typic (Cool, Summer Moist)

Representative Area: Middle Rockies—Uinta Mountains (MLRA 47 LRU C) in Utah and Wyoming; Southern Rockies in Colorado and Utah – MLRA 48A south of Colorado River and I-70; potential Gunnison sage-grouse in Colorado

Status of ESDs: MLRA 47 has site concept with no STM from Utah, closest thing with an STM is a site that is more xeric; MLRA 48A has a draft contemporary STM from Colorado and another site concept from Utah with no STM

1. R047XA430UT_MtnLoam-Provisional2012Xeric
2. R047XC430UT_MtnLoam-Provisional-noSTM
3. R048A228CO_MountainLoam_2015DRAFT
4. R048A247CO_DeepClayLoam_2015DRAFT
5. R048AY405UT_MtnLoam_Provisional-noSTM

iv. Frigid/Xeric (Cool, Winer Moist) – MLRA 47 Wasatch Mountains – this regime was covered in Chambers et al. (2014a) so no analysis was conducted

c. West-Central Semiarid Prairies

i. Frigid bordering on Cryic/Ustic bordering on Aridic (Cool bordering on Cold, Summer Moist bordering on Dry)

Representative Area: Northwestern Glaciated Plains—MLRA 52 in northern Montana

Status of ESDs: MLRAs 52 has several draft contemporary STMS representing the cooler phase of Frigid with more summer precipitation

1. R052XC205MT_Clayey_10_to_14_inch_pz_2005DraftCool
2. R052XC206MT_Dense_Clay_10_to_14_inch_pz_2005DraftCool
3. R052XC217MT_Silty_10_to_14_inch_pz_2005DraftCool

ii. Frigid/Ustic bordering on Aridic (Cool, Summer Moist bordering on Dry)

Representative Area: Northwestern Great Plains—LRA 58A in Montana and 58D in South Dakota, 58C in North Dakota

Status of ESDs: MLRA 58A, LRU C and LRU E represents most of eastern Montana with older vintage STMs; MLRA 58D has STMs from South Dakota to represent this regime (vintage?)

1. R058AC041MT_Clayey11-14ppz_Provisional
2. R058AC052MT_DenseClay11-14ppz_Provisional
3. R058AC054MT_Claypan11-14ppz_Provisional
4. R058AE002MT_Clayey10-14ppz_Provisional
5. R058DY011SD_Clayey_Provisional2009
6. R058DY013SD_Claypan_Provisional2010
7. R058DY015SD_ThinClaypan_Provisional2010

iii. Frigid/Ustic-Typic (Cool, Summer Moist)

Representative Area: Northwestern Great Plains—MLRA 60A in South Dakota

Status of ESDs: MLRA 54 has contemporary STM from North Dakota that may be applicable; MLRA 60A has several STMs from South Dakota (age uncertain)

1. R054XY021ND_Claypan_Provisional2011
2. R060AY011SD_Clayey-13-16ppz_Provisional2012
3. R060AY015SD_ThinClaypan_Provisional2012
4. R060AY018SD_DenseClay_Provisional2012
5. R060AY025SD_ShallowDenseClay_Provisional2012

iv. Mesic/Ustic bordering on Aridic (Warm, Summer Moist bordering on Dry)

Representative Area: Northwestern Great Plains—drier portions of MLRA 58B in Wyoming, but could also apply to warmer portions of MLRA 58A, LRU C in Montana

Status of ESDs: MLRA 58B has older vintage STMs from Wyoming

1. R058BY104WY_Clayey10-14NP_Provisional2005
2. R058BY122WY_Loamy10-14NP_Provisional2005
3. R058BY158WY_ShallowClayey10-14NP_ Provisional2005
4. R058BY162WY_ShallowLoamy10-14NP_ Provisional2005

v. Mesic/Ustic-Typic (Warm, Summer Moist)

Representative Area: Northwestern Great Plains—wetter portions of MLRA 58B in Wyoming near Black Hills

Status of ESDs: MLRA 58B has older vintage STMs from Wyoming

R058BY222WY_Loamy15-17NP_Provisional2005

tOO.WJLztf5l5FP(4,w;P4lkf5OwLWGkLwlOP4l

Annually tilled agriculture (cropland)

Source: USDA National Agricultural Statistics Service Cropland Data Layer. 2014. Published crop-specific data layer. UDSA-NASS, Washington, DC. http://nassgeodata.gmu.edu/CropScape/ [Accessed 16 Sept 2015].

Ecoregions

Source: U.S Environmental Protection Agency. 2016. Level II and III Ecoregions of North America. https://www.epa.gov/eco-research/ecoregions-north-america [Accessed 16 Sep 2015].

Precipitation and temperature data—30 year normals.

Source: PRISM Climate Group, Northwest Alliance for Computational Science and Engineering. 2016. 30-year Normals. http://prism.oregonstate.edu/normals [Accessed 16 Sept 2015].

Fire perimeters—Geomac

Source: Walters, S.P.; Schneider, N.J.; Guthrie, J.D. 2011. Geospatial Multi-Agency Coordination (GeoMAC) wildland fire perimeters, 2008. Data Series 612. Washington, DC: U.S. Department of the Interior, U.S. Geological Survey. 6 p. http://www.geomac.gov/ [Accessed 1 Feb 2016].

Fire perimeters—MTBS

Source: Eidenshink, J.; Schwind, B.; Brewer, K.; [et al.]. 2007. A project for monitoring trends in burn severity: Fire Ecology. 3: 3–21. http://www.mtbs.gov/nationalregional/burnedarea.html [Accessed 15 Sept 2015].

Greater sage-grouse breeding habitat model

Source: Doherty, K.E.; Evans, J.S.; Coates, P.S.; [et al.]. 2015. Importance of regional variation in conservation planning and defining thresholds for a declining species: A range-wide example of the greater sage-grouse. https://www.sciencebase.gov/catalog/folder/560ea672e4b0ba4884c5ebb7 [Accessed 6 Oct 2015].

Greater sage-grouse population index model

Source: Doherty, K.E.; Evans, J.S.; Coates, P.S.; [et al.]. 2015. Importance of regional variation in conservation planning and defining thresholds for a declining species: A range-wide example of the greater sage-grouse. https://www.sciencebase.gov/catalog/folder/560ea65de4b0ba4884c5ebb5 [Accessed 6 Oct 2015].

Greater sage-grouse lek data

Source: Western Association of Fish and Wildlife Agencies (WAFWA)

Contact: Tom Remington, WAFWA, 2700 W. Airport Way, Boise, ID 83705; remingtontom@msn.com.

Gunnison sage-grouse lek data

Source: Colorado Parks and Wildlife; Utah Division of Wildlife Resources

Contacts: Kathy Griffin, Colorado Parks and Wildlife, 711 Independent Ave., Grand Junction, CO 81505; kathy.griffin@state.co.us; Avery Cook, Utah Division of Wildlife Resources, 1594 West North Temple, Salt Lake City, UT 84116; averycook@utah.gov.

Gunnison sage-grouse range plus linkages shapefile

Source: Utah Division of Wildlife Resources [UDWR] 2012. Gunnison sage-grouse habitat GIS shapefiles for occupied and vacant-unknown habitat. Last updated March 2012. http://dwrcdc.nr.utah.gov/ucdc/downloadgis/disclaim.htm [Accessed 7 June 2016].

Source: Colorado Parks and Wildlife (CPW) 2015. Gunnison sage-grouse habitat and linkage zones. Last updated November 2015. http://www.fws.gov/coloradoes/GUSG/ [Accessed December 2015].

Human disturbance

Source: Human disturbance percent developed imperviousness: U.S. Geological Survey. 2014. NLCD 2011 Percent Developed Imperviousness (2011 Edition, amended 2014). Sioux Falls, SD: U.S. Department of the Interior, Geological Survey. http://www.mrlc.gov/nlcd11_data.php [Accessed 11 May 2016]

Land cover—conifer (GRSG)

Source: U.S. Geological Survey (USGS). 2012. LANDFIRE 1.3.0 Existing Vegetation Type layer. Updated 12/17/2014. Washington, DC: U.S. Department of the Interior, Geological Survey. http://landfire.cr.usgs.gov/viewer/ [Accessed 26 Aug 2015].

Land cover—conifer (GUSG)

Source: Falkowski, M.J.; Evans, J.S.; Naugle, D.E.; [et al.]. [In press]. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management. http://dx.doi.org/10.1016/j.rama.2016.08.002 [Accessed 1 11511 5151].

Land cover—sagebrush

Source: U.S. Geological Survey (USGS). 2012. LANDFIRE 1.3.0 Existing Vegetation Type layer. Updated 12/17/2014. Washington, DC: U.S. Department of the Interior, Geological Survey. http://landfire.cr.usgs.gov/viewer/ [Accessed 26 Aug 2015].

Land ownership

Source: Surface Management Agency. Complied and maintained by the Department of the Interior, Bureau of Land Management. 2015. http://www.geocommunicator.gov/GeoComm/ [Accessed 7 May 2016].

Oil and gas wells

Source: Point density analysis conducted by the Bureau of Land Management and derived from AFMSS currently active oil and gas well points 2015; IHS currently active oil and gas well points 2015. https://www.ihs.com/products/us-well-data.html [Accessed 11 May 2016].

Roads

Source: Line density analysis conducted by the Bureau of Land Management and derived from ESRI street maps premium. Copyright © 1995–2014 ESRI. All rights reserved. Published in the United States of America. Online: http://www.esri.com/data/streetmap [Accessed 11 May 2016].

Soil data (SSURGO)

Source: Soil Survey Staff. 2014a. Soil Survey Geographic (SSURGO) Database. U.S. Department of Agriculture, Natural Resources Conservation Service. http://sdmdataaccess.nrcs.usda.gov/ [Accessed 3 Oct 2015].

Soil data (STATSGO)

Source: Soil Survey Staff. 2014b. Soil Survey Geographic (STATSGO2) Database. U.S. Department of Agriculture, Natural Resources Conservation Service. http://sdmdataaccess.nrcs.usda.gov/ [Accessed 3 Oct 2015].

Soil temperature and moisture regime

Source: Campbell, S.B. 2016. Soil temperature and moisture regimes across sage-grouse range. Data product. Portland, OR: U.S. Department of Agriculture, Natural Resources Conservation Service. https://www.sciencebase.gov/catalog/item/538e5aa9e4b09202b547e56c [Accessed 10 May 2016].

Understanding landscape concepts of plant cover relative to typical management concepts of plant cover is important for prioritizing lands for management of sage-grouse. Ground-based measurements of sagebrush canopy cover (for example, using line-intercept measurements) should not be confused with landscape cover due to vast differences in measurement scale (e.g., square meters for management units and square kilometers for landscapes).

A landscape is defined rather arbitrarily as a large area in total spatial extent, somewhere in size between sites (acres or square miles) and regions (100,000s of square miles). The basic unit of a landscape is a patch, which is defined as a bounded area characterized by a similar set of conditions. A habitat patch, for example, may be the polygonal area on a map representing a single land cover type. Landscapes are composed of a mosaic of patches. The arrangement of these patches (the landscape configuration or pattern) has a large influence on the way a landscape functions and for landscape species, such as sage-grouse, sagebrush habitat patches are extremely important for predicting if this bird will be present within the area (Connelly et al. 2011).

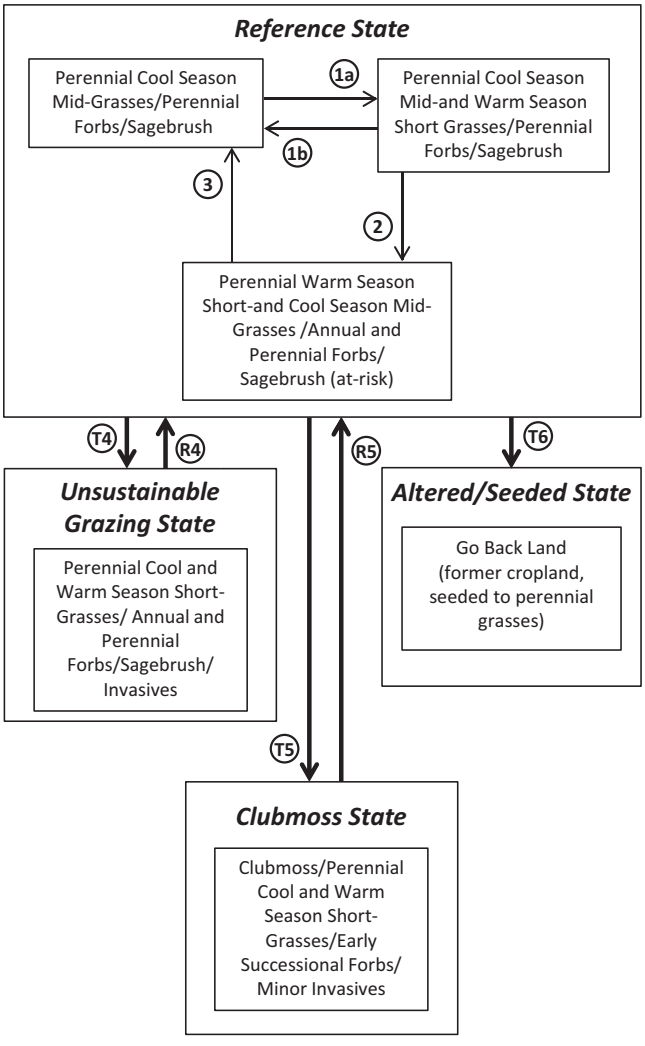
Remotely sensed data of land cover is typically used to represent landscapes. These data may combine several sources of data and may include ancillary data, such as elevation, to improve the interpretation of data. These data are organized into pixels that contain a size or grain of land area. For example, Landsat Thematic Mapper spectral data used in determining vegetation cover generally have pixels that represent ground areas of 900 m^2 (30 m x 30 m). Each pixel's spectral signature can be interpreted to determine what type of vegetation dominates that pixel. Groups of adjacent pixels with the same dominant vegetation are clustered together into polygons that form patches.

Landscape cover of sagebrush is determined initially by using this vegetation cover map, but a "rolling window" of a predetermined size (e.g., 5 km^2 or 5,556 pixels that are 30 m by 30 m in size) is then moved across the region one pixel at a time to smooth the data. In this process, the central pixel of the "window" is reassigned a value equal to the proportion of pixels in the window for which sagebrush is the dominant vegetation. The process is repeated until the value for each pixel within the analysis region has been reassigned to represent the landscape cover of sagebrush within a 5-km^2 window.

Desert

The characteristics and relative resilience and resistance of the ecological types in the state-and-transition models are in table 3. Large boxes illustrate states that are comprised of community phases (smaller boxes). Transitions among states are shown with arrows starting with T; restoration pathways are shown with arrows starting with R. The "at risk" community phase is most vulnerable to transition to an alternative state.

A.6.1 West Central Semiarid Prairies
Frigid bordering on Cryic/Ustic bordering on Aridic
Grass Dominated w/ SilverSagebrush (10-14 in PZ)
High Resilience and Resistance



1a Sagebrush increases and proportion of cool season mid-grass Functional/Structural Group decreases due to disturbances such as drought (3-5 years) and spring grazing.

1b Normal precipitation patterns favor herbaceous understory. Grazing intensity and/or duration is reduced to allow for herb recovery.

2 Sagebrush increases and proportion of cool and warm season mid-and short-grass Functional/ Structural Groups increases due to prolonged drought (5-7 years), increased grazing intensity and duration, and lack of fire. Plant community is at-risk of leaving reference state with extended drought and continued grazing pressure.

3 With favorable precipitation, disturbance such as fire, and a grazing system that provides rest and recovery of preferred species, cool season mid-grass Functional/Structural Groups increase.

T4 Extended drought (>7 years) along with high intensity and long duration grazing result in transition to a state resistant to grazing that is dominated by cool and warm season short-grass Functional/Structural Groups. Silver sagebrush cover is at its highest, and early seral forbs are present. There is potential for invasive species such as field brome in high moisture years and/or due to removal of grazing, lack of fire, and other conditions causing accumulation of excessive litter.

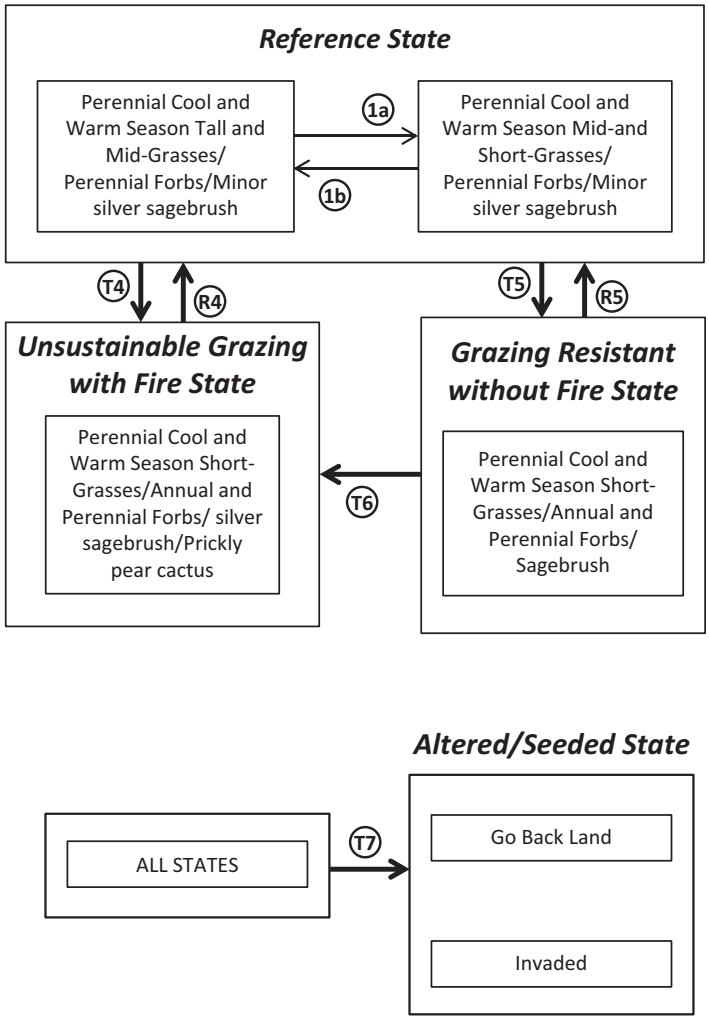
R4 Normal precipitation patterns, fire or fire surrogates (herbicides and/or mechanical treatments), and a grazing regime with proper timing and intensity that varies season of use can return the site to the reference state.

T5 Extended drought (>7 years) may result in dense stands of clubmoss. However, no grazing, light grazing, and rotational grazing combined with drought can result in more rapid increase in clubmoss than drought alone. Lack of fire may contribute to this transition as well. Potential for invasives such as field brome is minor, and this transition occurs more often on older, more developed soils with an argillic horizon.

R5 Extended periods of normal and above average precipitation, mechanical renovation, chemical treatment, fertilizer/manure application, seeding (if an adequate seedbank does not exist), fire, and/or periods of rest or light grazing can return the site to the reference state.

T6 Former cropland seeded to introduced and/or native perennial grasses, largely funded by government programs. In the 1960-1970s seedings were primarily introduced species such as crested wheatgrass, intermediate wheatgrass, and smooth brome. From 1985 to present both introduced and native species were used, mainly under the Conservation Reserve Program. Sagebrush is largely absent from this state. There is potential for invasive species such as field brome in high moisture years and/or due to removal of grazing, lack of fire, and other conditions that would result in an accumulation of excessive litter.

A.6.2 West Central Semiarid Prairies
Frigid/Ustic Grass Dominated (13-18 in PZ)
Moderate to High Resilience and Resistance



1a Proportion of cool and warm season tall and mid-grass Functional/Structural Groups decreases due to disturbances such as drought and spring grazing with a lack of disturbances such as fire.

1b Fire and normal precipitation patterns favor herbaceous understory. Reduced grazing intensity and/or duration allows for herbaceous recovery.

T4 Extended drought, high intensity and long duration grazing, and a normal fire regime or fire surrogate (herbicides and/or mechanical treatments) will result in a transition to a grazing resistant state dominated by warm and cool season short-grass Functional/Structural Groups and silver sagebrush and prickly pear cactus. Forbs are early seral.

R4 Normal precipitation patterns and proper timing and intensity of grazing that varies season of use can return the site to the reference state. Mechanical treatments are often used to renovate and return the site to one resembling the reference state.

T5 Extended drought, high intensity and long duration grazing, and lack of fire will result in a transition to a grazing resistant state dominated by short-statured warm and cool season grasses. Forbs are early seral.

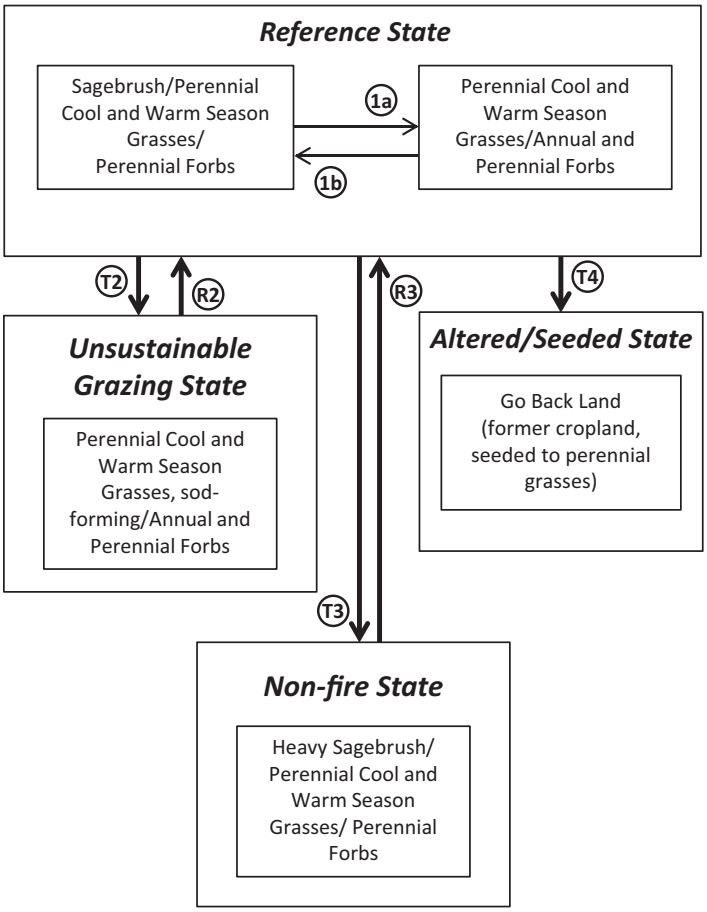
R5 Extended periods of normal precipitation, possibly seeding (if an adequate seedbank does not exist), mechanical renovation, and reduced grazing pressure that varies season of use can return the site to one resembling the reference state.

T6 Introduction of fire results in loss of Wyoming big sagebrush and an increase in silver sagebrush. Continued high intensity and long duration grazing results in the increase of undesirable species like prickly pear cactus.

T7 Former cropland seeded to introduced and/or native perennial grasses, largely funded by government programs. In the 1960-1970s seedings were primarily introduced species such as crested wheatgrass, intermediate wheatgrass, and smooth brome. From 1985 to present seedings used both introduced and native species, mainly under the Conservation Reserve Program. An invaded plant community is possible if seed source is introduced or adjacent to area. Dominant species include field brome, smooth brome, Kentucky bluegrass, thistles, bindweed, knapweed, leafy spurge, hoary cress, and other introduced weedy species. Sagebrush is largely absent from this state.

A.6.3 West Central Semiarid Prairies Frigid/Ustic bordering on Aridic Wyoming Big Sagebrush (10-14 in PZ)

Moderate to High Resilience and Resistance



1a Sagebrush decreases due to fire and normal precipitation patterns that favor the herbaceous understory. Grazing intensity and/or duration is reduced to allow for herbaceous recovery.

1b Sagebrush increases and proportion of cool season grasses decrease due to disturbances such as drought and grazing, along with a lack of disturbances such as fire.

T2 Prolonged drought, improper grazing, and frequent sagebrush control using fire or fire surrogates (herbicides and/or mechanical treatments) will result in transition to a grazing resistant state dominated by warm and cool season short-and sod-forming grass Functional/ Structural Groups and undesirable species such as prickly pear cactus. Invasive species (e.g., cheatgrass, field brome) can occur in disturbed areas. Field brome invasion can occur in undisturbed rangelands at the upper end of the precipitation range.

R2 Normal precipitation patterns, reducing the frequency and severity of disturbances that kill sagebrush, and proper timing and intensity grazing regime that varies season of use can return the site to the reference state.

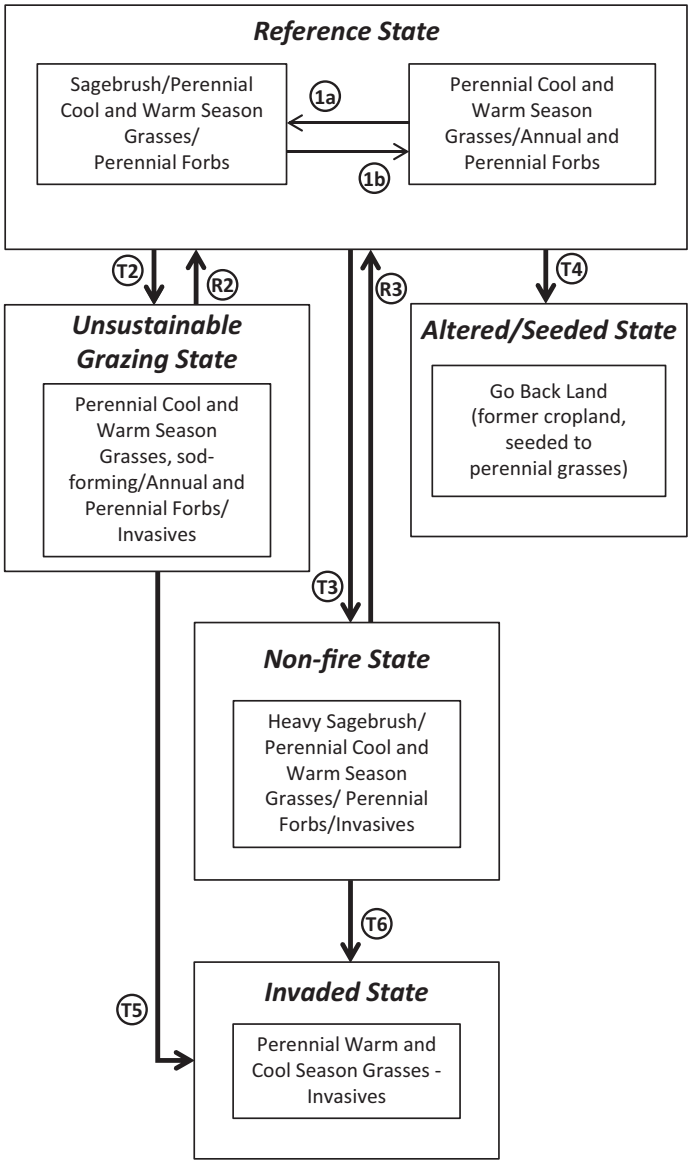
T3 Extended drought, frequent and severe grazing, and removal of fire and fire surrogates (herbicides and/or mechanical treatments) will result in transition to a state dominated by sagebrush with minor warm and cool season short-grass and forb Functional/Structural Groups. Invasion can occur as bare ground increases in sagebrush canopy interspacesin disturbed areas.

R3 Extended periods of normal precipitation, treatment with fire surrogates, seeding (if adequate seedbank does not exist), and reduced grazing pressure that varies season of use can return the site to the reference state.

T4 Former cropland that has been seeded to introduced and/or native perennial grasses, largely funded by government programs. In the 1960-1970s seedings were primarily introduced species such as crested wheatgrass, intermediate wheatgrass, and smooth brome. From 1985 to present both introduced and native grasses were used, mainly under the Conservation Reserve Program. Sagebrush is largely absent.

A.6.4 West Central Semiarid Prairies Mesic/Ustic bordering on Aridic Wyoming Big Sagebrush (10-14 in PZ)

Low to Moderate Resilience and Resistance



1a Sagebrush increases and proportion of cool season grasses decrease due to disturbances such as drought and grazing with a lack of disturbances such as fire.

1b Sagebrush decreases due to fire and normal precipitation patterns that favor an herbaceous understory. Reduced grazing intensity and/or duration allows for herbaceous recovery.

T2 Extended drought, frequent and severe grazing, and frequent sagebrush control using fire or fire surrogates result in a transition to a grazing resistant state dominated by warm and cool season short-and sod-forming grass Functional/Structural Groups and undesirable species such as prickly pear cactus. Invasion of cheatgrass and/or field brome can occur.

R2 Normal precipitation that reduces the frequency and severity of sagebrush killing disturbances, and proper timing and intensity grazing that varies season of use can return the site to the reference state.

T3 Extended drought, frequent and severe grazing, and removal of fire and fire surrogates will result in transition to a state dominated by sagebrush with minor warm and cool season short-grass and forb Functional/ Structural Groups. Invasion often occurs as bare ground increases in sagebrush canopy interspaces.

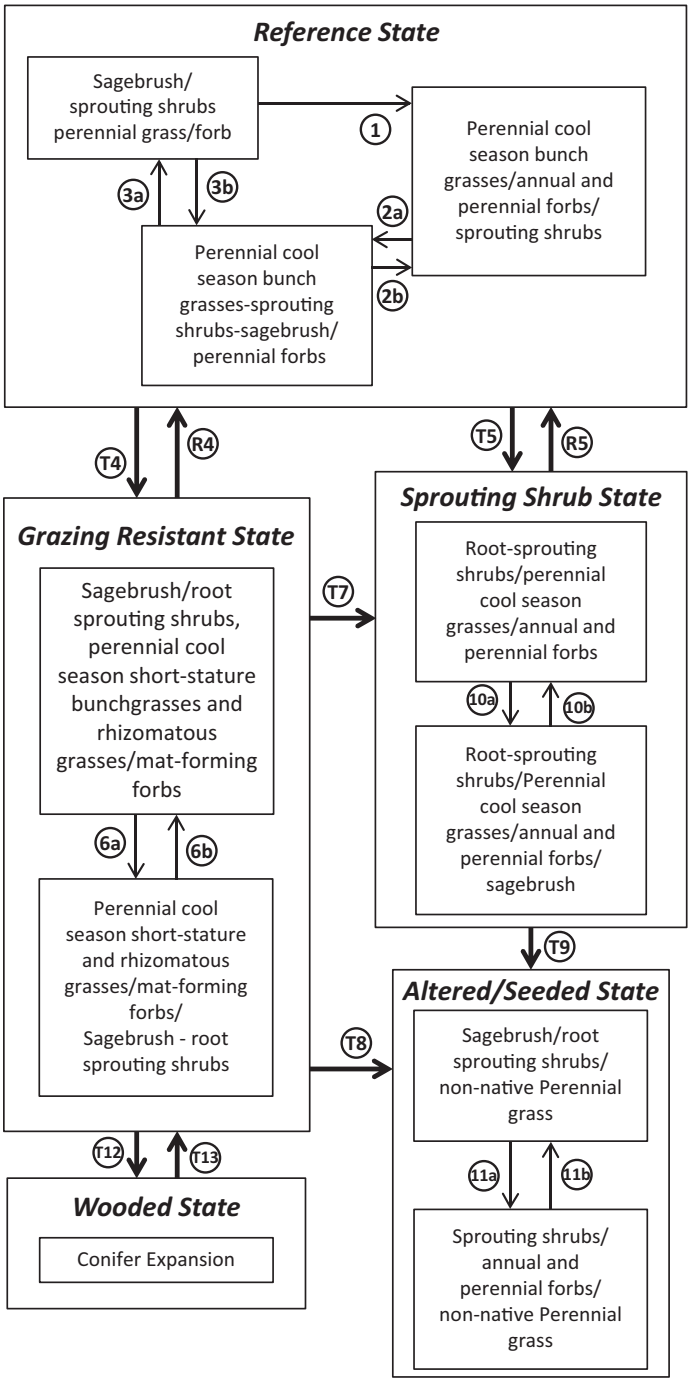
R3 Extended periods of normal precipitation, treatment with fire surrogates, seeding (if adequate seedbank does not exist), and reduced grazing pressure that varies season of use can return the site to the reference state.

T4 Former cropland that has been seeded to introduced and/or native perennial grasses, largely funded by government programs. In the 1960-1970s seedings were primarily introduced species such as crested wheatgrass, intermediate wheatgrass, and smooth brome. From 1985 to present seedings used both introduced and native grasses, mainly under the Conservation Reserve Program. Sagebrush is largely absent.

T5 Fire and fire surrogates, followed by warm and wet springs and year-long grazing can result in an T6 invaded state co-dominated by annual grasses (cheatgrass) and short-stature warm and cool season perennial grasses. Shrubs are largely absent.

A.6.5 Western Cordillera – Cryic/Typic Ustic Mountain Big Sagebrush/ Mixed Mountain Shrubs (15 -19 in+ PZ)

High Resilience and Resistance



1 Perennial grass, forbs and sprouting shrubs increase and dominate due to disturbances that decrease sagebrush, primarily wildfire.

2a Sagebrush and other shrubs increase with time until co-dominant with herbaceous species.

2b Perennial grass, forbs, and sprouting shrubs increase due to disturbances that decrease sagebrush, e.g., wildfire, insects, and disease.

3a Sagebrush and other shrubs increase with time.

3b Perennial grass, forbs, and sprouting shrubs increase due to minor disturbances that decrease sagebrush like cool fire, insects, and disease.

T4 Continuous grazing with cattle during the critical growth period of cool season grasses results in dominance of sagebrush and an increase in grazing tolerant native forbs (e.g., lupine, pussy-toes). As bare ground increases, surface erosion (e.g., rills, sheet erosion) may occur, resulting in loss of the surface soil horizon, and pedestalled plants.

R4 Sagebrush treatment via chemical, mechanical, or prescribed fire combined with a grazing system that allows periodic deferment during the critical growth period can result in return to the reference.

T5 Increased disturbance frequency and/or intensity (e.g., fire, fire surrogates, and/or mechanical types of disturbance, and/or high density/frequency grazing) will result in dominance of root-sprouting shrubs.

R5 Removal of disturbances and a grazing regime that allows for adequate rest and recovery of native perennial grasses and forbs can eventually result in a return to the reference state.

6a Perennial cool season short-stature bunchgrasses and rhizomatous grasses, mat-forming forbs, and sprouting shrubs increase in dominance due to disturbances that decreased sagebrush (e.g., wildfire, insects, disease).

6b Sagebrush, non-browsed shrubs, and mat-forming forbs increase with time.

T7 An increase in disturbance frequency, fire, fire surrogates, mechanical types of disturbance and/or high density/ frequency grazing will result in dominance of root-sprouting shrubs.

T8 Introduction of grazingtolerant non-native species, such as Kentucky bluegrass during homesteading days or smooth brome during reclamation results in transition to this state.

T9 Grazing tolerant non-native species are seeded, and disturbances are removed reducing sagebrush.

10a Sagebrush and other shrubs increase.

10b Perennial grass, forbs, and sprouting shrubs increase due to disturbances that decrease sagebrush (e.g., wildfire, insects, disease).

11a Sprouting shrubs, forbs, and non-native perennial grasses increase due to disturbances that decrease sagebrush (e.g., wildfire, insects, disease) or treatments that remove or reduce sagebrush.

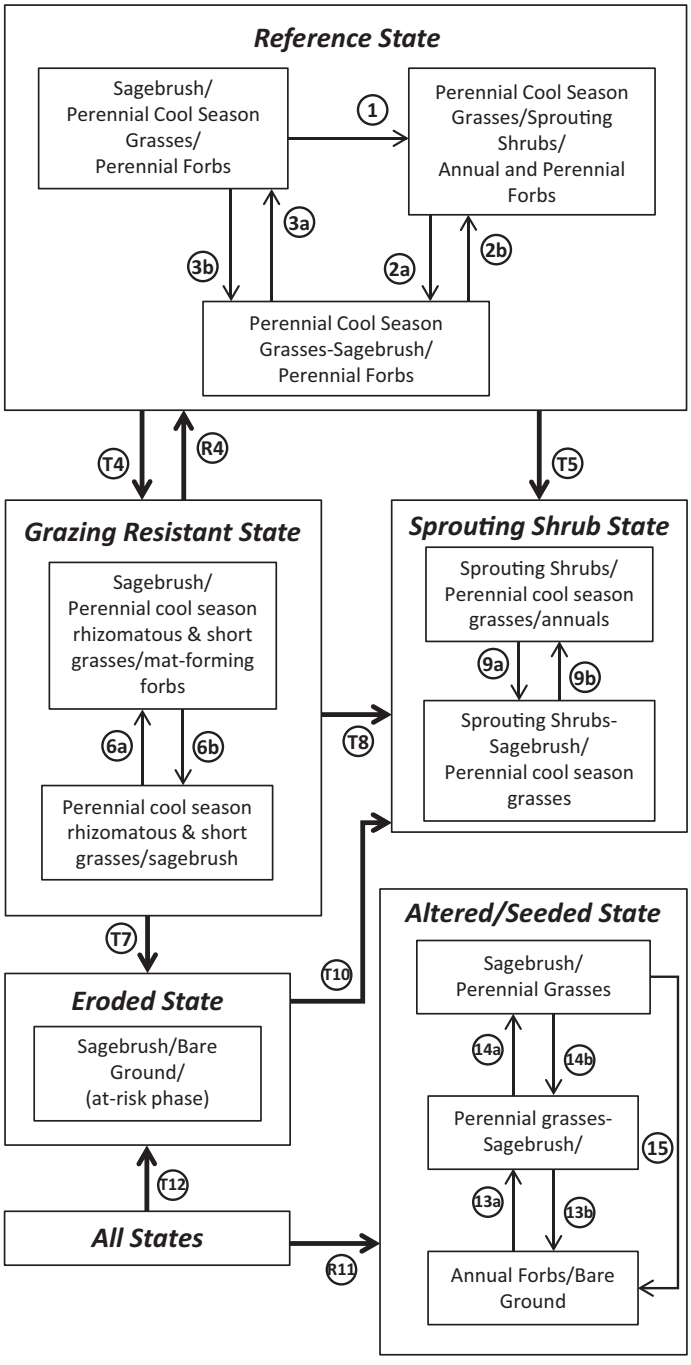
11b Sagebrush and other shrubs increase.

T12 High levels of fuel reduction through grazing and fire suppression can lead to conifer expansion outside the normal range of variability for a site.

T13 Above average precipitation and/or reduced grazing pressure allow fine fuel accumulation, and the use of fire or fire surrogates can result in return to the Grazing Resistant State, but return to the Reference State is only achievable through (R4) with the appropriate grazing prescription.

A.6.6 Cold Deserts – Frigid bordering on Cryic/Ustic bordering on Aridic Wyoming Big Sagebrush (9-14 in PZ)

Moderate to Low Resilience and Moderately High Resistance



1 Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens. Fire is rare.

2a Sagebrush increases with time until it is co-dominant with the herbaceous understory.

2b Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens.

3a Sagebrush increases with time until dominant.

3b Perennial grass and forbs increase due to minor disturbances that decrease sagebrush.

T4 Continuous spring grazing during the critical growth period of cool season grasses results in dominance of grazing tolerant species, like short-statured bunchgrasses (e.g. Sandberg bluegrass) and rhizomatous species. As bare ground increases, surface erosion (e.g., rills, sheet erosion) and pedestalled plants (especially bunchgrasses) result.

R4 Light to moderate grazing with periodic rest during critical growth periods along with fire, herbicides, and/or mechanical treatments result in return to reference state.

T5 An increase in fire, fire surrogates, mechanical disturbance, and/or high density/frequency grazing results in disturbance-adapted sprouting shrubs like rabbitbrush.

6a Sagebrush increases with time until dominant.

6b Grazing tolerant perennial cool season grasses increase due to disturbances that decrease sagebrush.

T7 Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing by cattle, resulting in altered biotic, hydrologic, and soil function. This state is at-risk of invasion by annuals after a catastrophic sagebrush killing event.

T8 Chemical or mechanical treatments to reduce sagebrush in the 1940s through 70s followed by improper stocking rates and seasons of use resulted in a shift toward sprouting shrubs, such as rabbitbrush.

9a Sagebrush increases with removal of disturbances over time until co-dominant with sprouting shrubs.

9b Perennial cool season grasses and sprouting shrubs increase due to disturbances that decrease sagebrush.

T10 Chemical or mechanical treatments to reduce sagebrush in the 1940s through 70s followed by improper stocking rates and seasons of use resulted in a shift toward sprouting shrubs, such as rabbitbrush.

R11 All states are subject to disturbance from oil and gas exploration or other mechanical disturbances that remove surface soils. Restoration success on good soil management, proper seeding techniques, and weather. Due to native seed availability, grass and shrubs can be restored, but forb diversity and applicability to site conditions can be a limiting factor for biotic integrity. Something resembling the reference state may be achieved with key differences in soil and hydrologic function.

T12 Many abandoned oil and gas wells without proper reclamation practices (no top soil management/replacement or seeding) from the 1980s are now in the Eroded State.

13a Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory.

13b Perennial grass and forbs become dominant due to disturbances that decrease sagebrush.

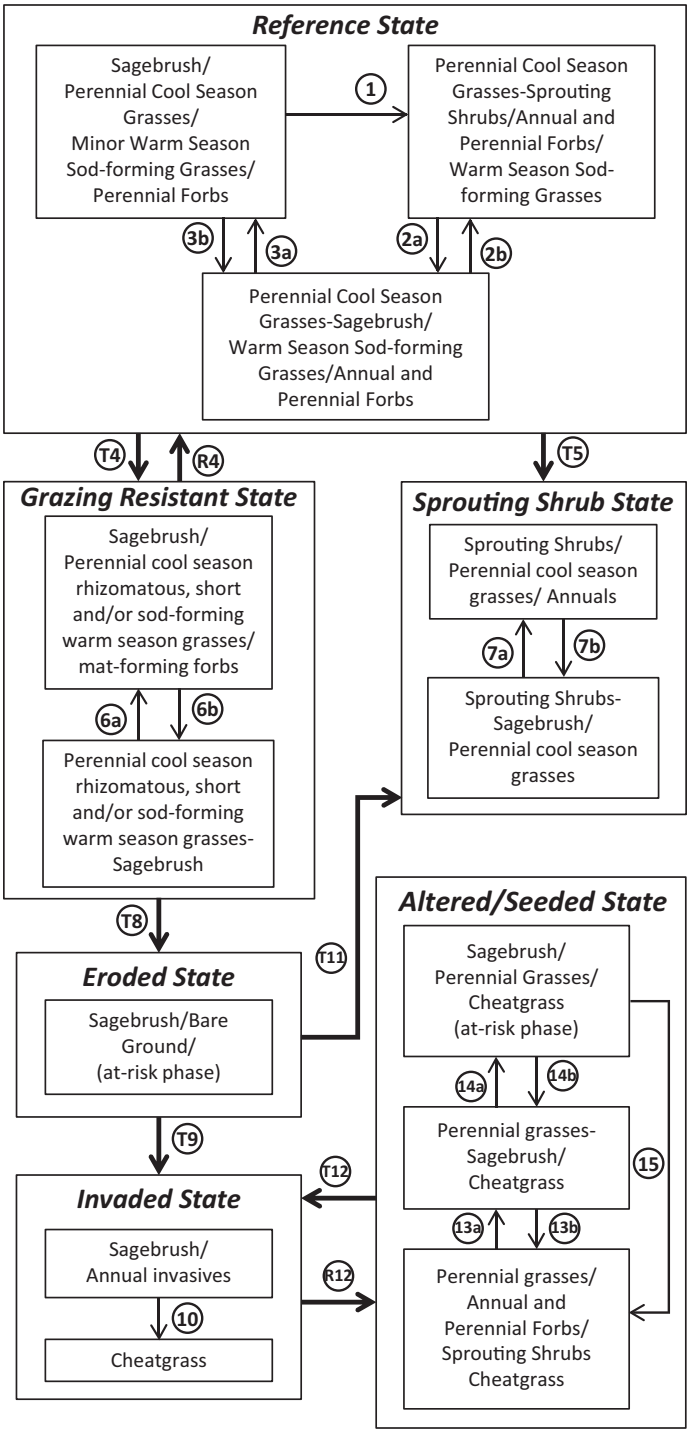
14a Sagebrush increases with no disturbances over time.

14b Perennial grass and forbs become dominant due to minor disturbances that decrease sagebrush.

15 Annual forbs become dominant due to disturbances that remove existing perennial vegetation.

A.6.7 Cold Deserts – Frigid/Ustic bordering on Aridic Wyoming Big Sagebrush (10-14 in PZ)

Moderate Resilience and Resistance



1 Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens.

2a Sagebrush increases with time until co-dominant with the herbaceous understory.

2b Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush.

3a Sagebrush increases with time until dominant.

3b Perennial grass and forbs increase due to disturbances that decrease sagebrush.

T4 Continuous spring grazing with cattle during the critical growth period of cool season grasses results in dominance of grazing tolerant species that may include warm season grasses (e.g., blue grama). As bare ground increases, surface erosion (e.g., rills, sheet erosion) and pedestalled plants (especially bunchgrasses) may result.

R4 Light to moderate grazing with periodic rest during critical growth periods along with fire, herbicides, and/or mechanical treatments can result in return to reference state.

T5 An increase in the disturbance cycle by fire, fire surrogates, mechanical types of disturbance, and/or high density/ frequency grazing will favor sprouting shrubs such as rabbitbrush. Annual invasives can occur.

6a Sagebrush increases with time. Cheatgrass and other weeds can be present, but do not dominate.

6b Perennial cool season grasses increase due to disturbances that decrease sagebrush. A temporary flush of annual invaders is expected.

7a Sagebrush increases with time and removal of disturbances until co-dominant with herbaceous understory.

7b Perennial cool season grasses and sprouting shrubs increase due to disturbances that decrease sagebrush.

T8 Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing by cattle, resulting in altered biotic, hydrologic, and soil function. This state is at-risk to invasion by annuals such as cheatgrass, especially after a stand-replacing, sagebrush killing event.

T9 If a cheatgrass seed source is introduced, and weather conditions are conducive to establishment (warm wet spring), it will invade, especially after a stand-replacing event that eliminates sagebrush.

10 Fire and fire surrogates that kill sagebrush will dramatically increase cheatgrass.

T11 Multiple chemical and/or mechanical treatments or biological disturbances that reduce sagebrush will result in a shift toward sprouting shrub dominance with potential for cheatgrass to invade.

T12 Catastrophic climatic events and/or fire can result in cheatgrass dominance, especially when in the sagebrush dominant phase of the altered state.

R12 A restoration treatment, including chemical treatment for cheatgrass and seeding can restore a perennial grass community and eventually support an altered sagebrush community with invaders.

13a Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory, but cheatgrass will be present.

13b Perennial grass and forbs become dominant due to disturbances that decrease sagebrush.

14a Sagebrush increases with time and no disturbances until dominant, but cheatgrass may be present.

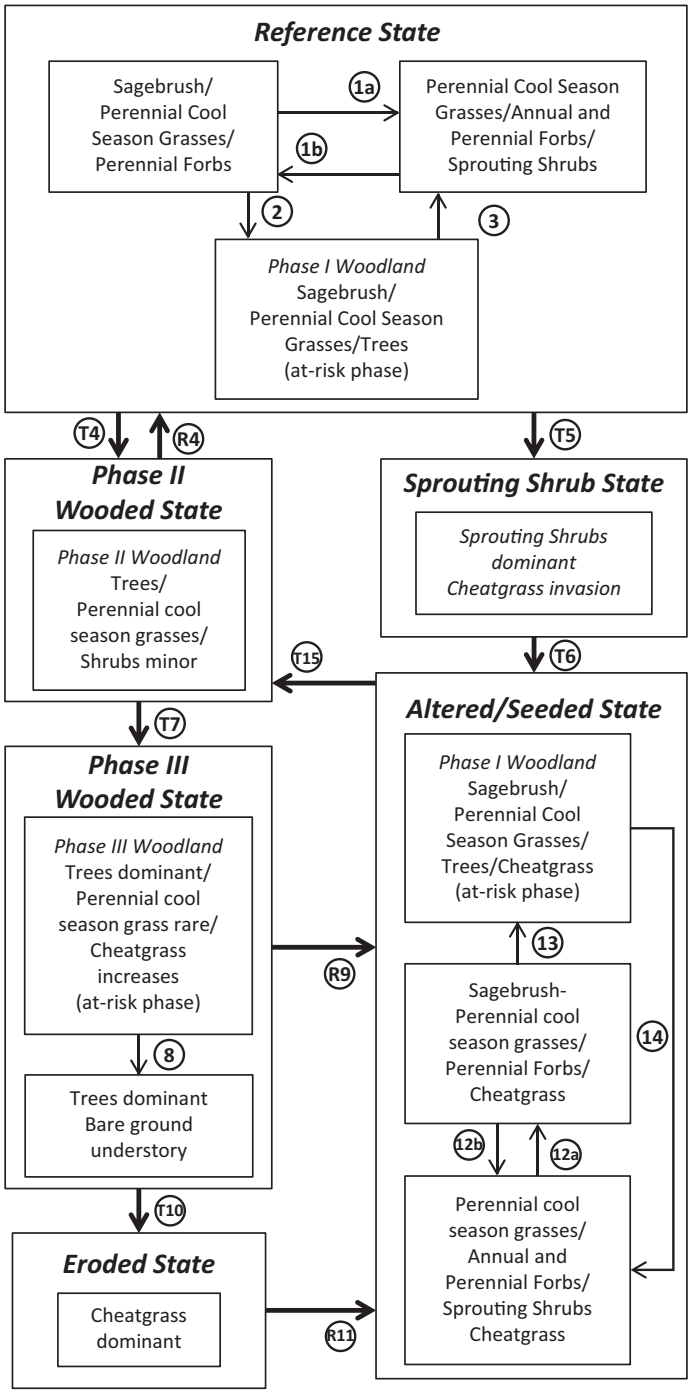
14b Perennial grass and forbs become dominant due to minor disturbances that decrease sagebrush.

15 Perennial grass and annual/perennial forbs become dominant due to disturbances that decrease sagebrush.

A.6.8 Cold Deserts – Frigid bordering on Mesic/Ustic Wyoming Big Sagebrush (14-18 in PZ)

Piñon pine and/or juniper potential

Moderate to High Resilience and Moderate Resistance



1a Disturbances such as wildfire, insects, disease, and pathogens result in less sagebrush and more perennial cool season grasses, forbs, and sprouting shrubs like rabbitbrush.

1b Sagebrush increases with time until dominant.

2 Time without fire or fire surrogates combined with seed sources for piñon and/or juniper trigger a Phase I Woodland invasion and an at-risk phase.

3 Fire and/or fire surrogates (herbicides and/or mechanical treatments) that remove trees may restore perennial cool season grasses and forbs, but these activities often also reduce sagebrush temporarily.

T4 Increasing tree abundance results in a Phase II woodland with decreasing sagebrush cover due to competition for sunlight, water and nutrients, and a transition to a tree- dominated state. Cheatgrass invasion is common during this transition.

R4 Fire and fire surrogates (herbicides and/or mechanical treatments) that remove trees may restore perennial cool season grasses, annual/perennial forbs, and eventually sagebrush dominance if treated during Phase II invasion.

T5 An increase in fire, fire surrogates, mechanical types of disturbance and/or high density/frequency grazing will favor sprouting shrubs like rabbitbrush. Cheatgrass often invades.

T6 Removal of disturbances can result in a restored state over time. Seeding may be necessary depending on the type and amount of disturbance.

T7 Infilling of trees and/or improper grazing can result in further increase in tree canopy cover, resulting in near complete loss of sagebrush component, decreased perennial cool season grasses, and increased risk of high severity crown fires. Cheatgrass will likely increase with favorable climate conditions.

8 As crown canopy increases, all other vegetation, including perennial understory and cheatgrass decrease until trees are almost the only remaining vegetation.

R9 Seeding after fire or fire surrogates may be necessary on sites with depleted perennial cool season grasses, forbs, and shrubs. If soils are not highly altered and native species seeded, it is possible to transition to a state that is similar to the Reference State, but with altered biotic function.

T10 Catastrophic fire without proper rehabilitation can result in an abiotic hydrologic and biotic threshold crossing to an eroded state depending on soils, slope, and understory species. Key soil properties can change, altering site potential. Cheatgrass dominates the system and it burns before perennial vegetation becomes established.

R11 Seeding after catastrophic fire or fire surrogates will be necessary due to lack of a perennial cool season grass, forb, and shrub seedbank. Seeding with nonnatives may decrease annual invasives, but will also reduce native species. Biotic and hydrologic function may be irreversibly altered. Restoration could be cost prohibitive.

12a Disturbances result in less sagebrush and more perennial cool season grasses, forbs, and sprouting shrubs like rabbitbrush. Increases is soil water and nutrient availability result in increased cheatgrass.

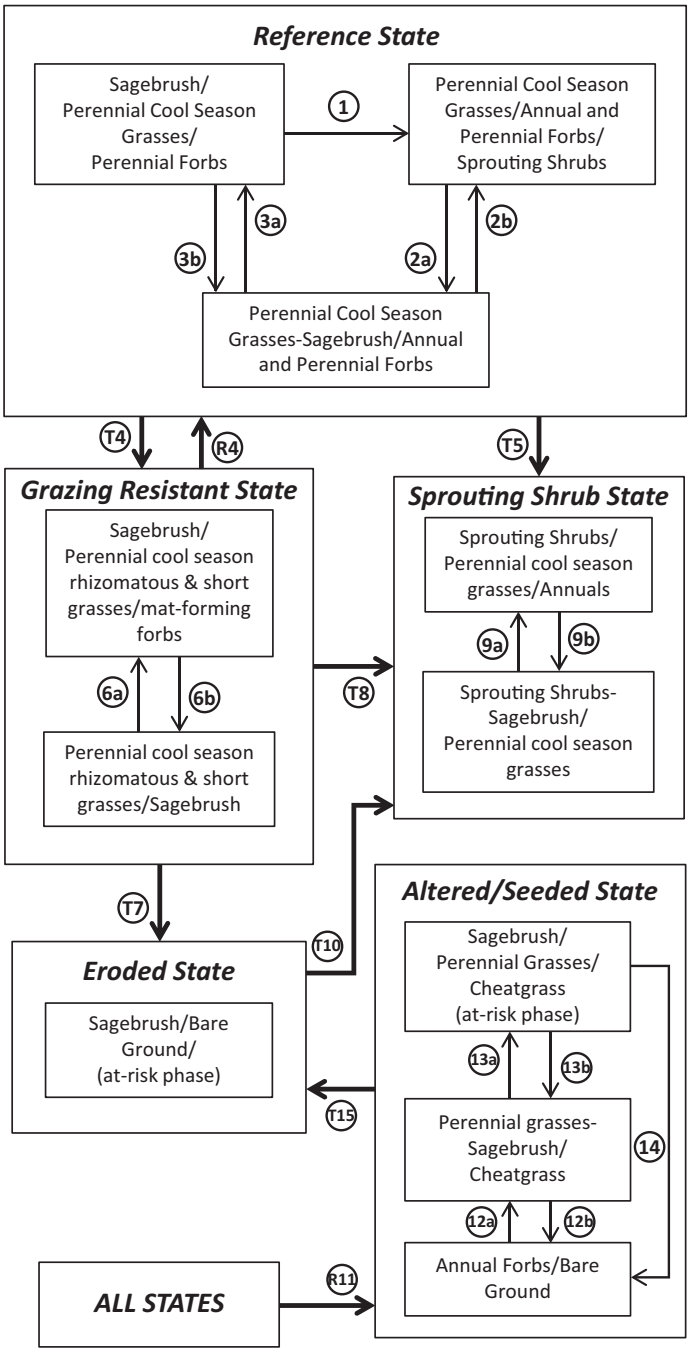
12b Sagebrush increases until co-dominant with the herbaceous species. Cheatgrass decreases, but is present.

13 Time combined with seed sources for piñon and/or juniper trigger a Phase I Woodland and an at-risk phase.

14 Fire and or fire surrogates (herbicides and/or mechanical treatments) that remove trees may restore perennial cool season grasses and annual/perennial forbs, but these activities often reduce sagebrush and increase cheatgrass temporarily.

T15 Increasing tree abundance results in a Phase II woodland with decreasing sagebrush due to competition, resulting in a transition to a Phase I Wooded State.

A.6.9 Cold Deserts – Frigid/Aridic bordering on Ustic
Wyoming Big Sagebrush (7-10 in PZ)
Moderate to Low Resilience and Moderate Resistance



(1) Perennial grass and forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens. Fire is rare in this system.

(2a) Sagebrush increases with time until co-dominant with the herbaceous understory.

(2b) Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens. Fire is rare.

(3a) Sagebrush increases with time until dominant.

(3b) Perennial grass and forbs increase due to minor disturbances that decrease sagebrush.

(T4) Continuous spring grazing with cattle during the critical growth period of cool season grasses results in dominance of grazing tolerant species which may include warm season grasses (e.g., blue grama). As bare ground increases, surface erosion (e.g., rills, sheet erosion and pedestalled plants [especially bunchgrasses] result.

(R4) Light to moderate grazing that includes periodic rest during critical growth periods along with herbicide and/or mechanical treatments can result in return to the Reference State.

(T5) An increase mechanical treatments, high density/frequency grazing, or fire/fire surrogates will favor sprouting shrubs such as rabbitbrush and/or greasewood. Fire is rare. Cheatgrass can occur.

(6a) Sagebrush increases with time. Cheatgrass is often present with other weedy species.

(6b) Perennial cool season grasses increase due to disturbances that decrease sagebrush. Cheatgrass is often present with other weedy species.

(T7) Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing, resulting in altered biotic, hydrologic, and soil function. This state is at-risk to invasion by annual grasses.

(T8) Multiple chemicalor mechanical treatments, or biological disturbances to reduce sagebrush can result in a shift toward sprouting shrub dominance with potential for cheatgrass to invade.

(9a) Sagebrush increases with time and removal of disturbances until co-dominant with sprouting shrubs.

(9b) Perennial cool season grasses, sprouting shrubs, and annuals increase due to disturbances that decrease sagebrush.

(T10) Multiple treatments of chemical, mechanical, or biological disturbances to reduce sagebrush will result in a shift toward sprouting shrub dominance with potential for cheatgrass to occur.

(R11) A restoration treatment, including chemical treatment for cheatgrass and seeding can restore a perennial grass community and eventually support an altered sagebrush community with some invaders.

(12a) Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory, but cheatgrass may be present.

(12b) Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush like drought, freezing, flooding, insects, disease, and pathogens. There may be a temporary flush of annuals.

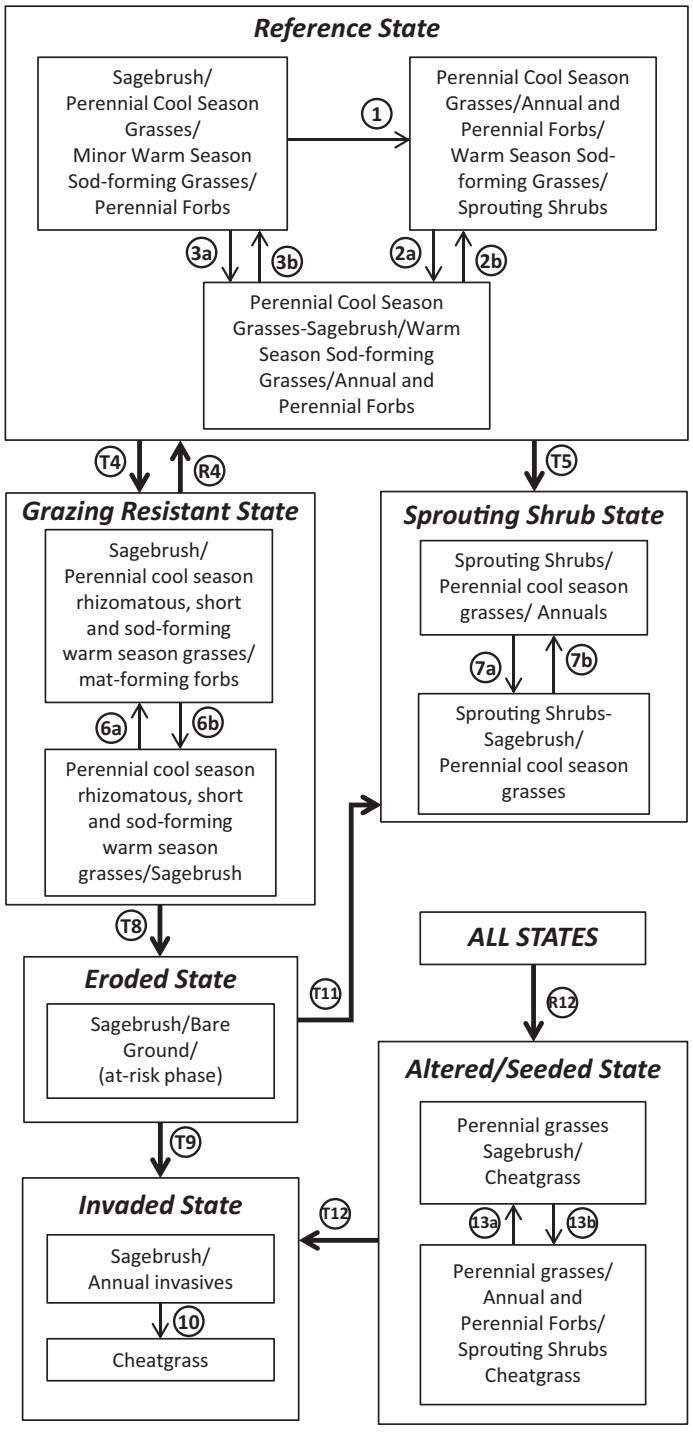
(13a) Sagebrush increases with time and no disturbances until dominant, but cheatgrass will be present.

(13b) Perennial grass and forbs become dominant due to minor disturbances that decrease sagebrush. There may be a temporary flush of annuals.

(14) Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush. There may be a temporary flush of annuals.

(T15) Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing, resulting in altered biotic, hydrologic, and soil function. Cheatgrass is often present in the understory, and could be considered an "invaded" state, except that it does not alter fire regimes and ecological dynamics of the site.

A.6.10 Cold Deserts – Mesic/Aridic bordering on Ustic
Wyoming Big Sagebrush (8-12 in PZ)
Moderate to Low Resilience and Low Resistance



1 Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens.

2a Sagebrush increases with time until co-dominant with the herbaceous understory.

2b Perennial grass and forbs become dominant due to disturbances that decrease sagebrush.

3a Sagebrush increases with time until dominant.

3b Perennial grass and forbs increase due to minor disturbances that decrease.

T4 Continuous spring grazing with cattle during the critical growth period of cool season grasses results in dominance of grazing tolerant species and increases in warm season species. As bare ground increases, surface erosion (e.g., rills, sheet erosion) and pedestalled plants (especially bunchgrasses) result.

R4 Light to moderate grazing that includes periodic rest during critical growth periods along with fire, herbicides, and/or mechanical treatments can restore perennial cool season perennial grasses and eventually sagebrush.

T5 An increase in fire, fire surrogates, mechanical types of disturbance, and or high density/frequency grazing favors sprouting shrubs like rabbitbrush. Cheatgrass can invade.

6a Sagebrush increases with time until dominant. Cheatgrass and other weedy species are often present.

6b Perennial cool season grasses increase due to disturbances that decrease sagebrush.

7a Sagebrush increases with time and removalof disturbances until co-dominant with sprouting shrubs.

7b Perennial cool season grasses and sprouting shrubs increase in dominance due to disturbances that decrease sagebrush.

T8 Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing, resulting in altered biotic, hydrologic, and soil function. This state is at-risk to invasion by annuals such as cheatgrass, especially with loss of sagebrush.

T9 If a cheatgrass seed source is introduced, and climatic conditions are conducive to establishment (warm wet spring), cheatgrass will invade.

10 A sagebrush killing event, such as fire and fire surrogates results in conversion to cheatgrass. Some perennial species may be present, but the system dynamics will be driven by annual invasives.

T11 Multiple treatments of chemical, mechanical, or biological disturbances to reduce sagebrush will result in a shift toward sprouting shrub dominance with potential for cheatgrass to occur.

T12 Catastrophic climatic events and/or fire can result in cheatgrass dominance, especially when in the sagebrush dominant phase of the altered state.

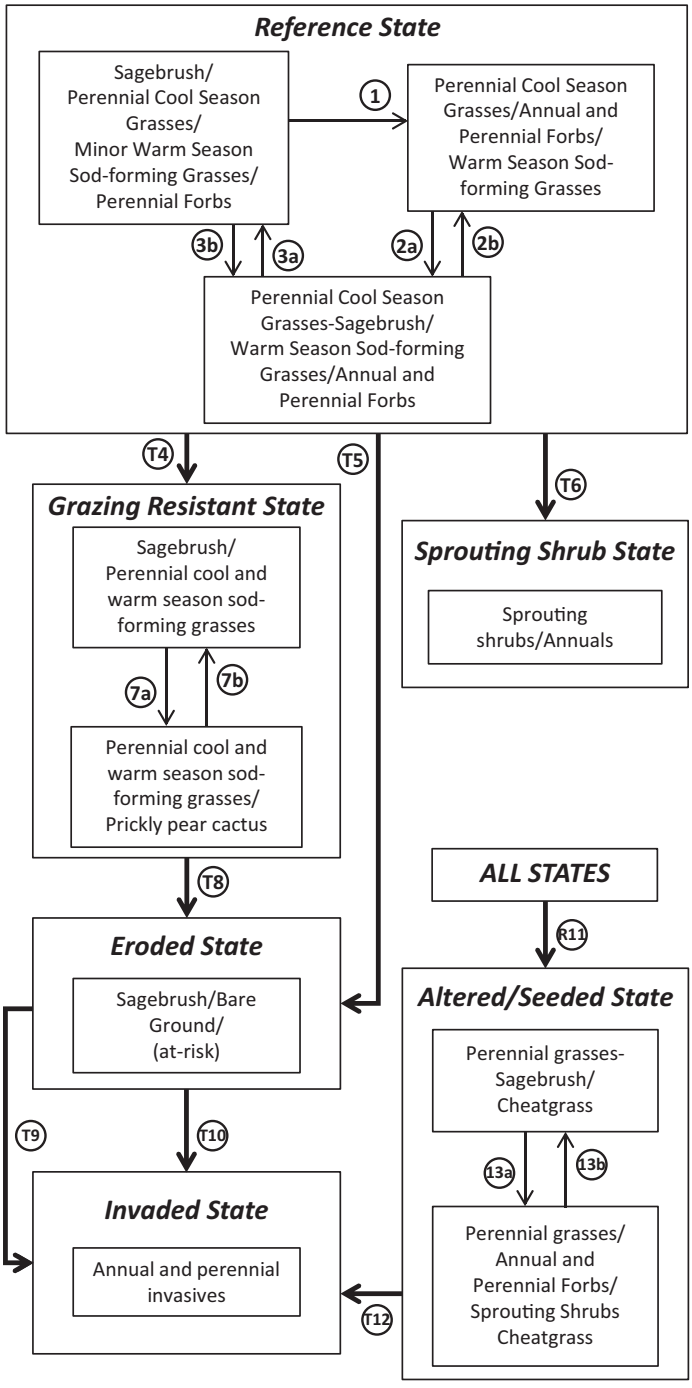
R12 A restoration treatment after severe ground disturbing activities, including mechanical treatment, seeding with non-native perennials can restore a perennial grass community and eventually support an altered sagebrush community with some invaders present. Sagebrush will be slow to reestablish.

13a Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory, but cheatgrass will be present.

13b Perennial grass and forbs become dominant due to disturbances that decrease sagebrush. There will likely be a temporary flush in annual invasives.

(T16) A restoration treatment after ground disturbing activities, including mechanical treatment, seeding with native perennials adapted to site conditions can result in a perennial grass community and eventually support an altered sagebrush community with some invaders present. Sagebrush will be slow to reestablish.

A.6.11 Cold Deserts – Mesic/aridic
Wyoming big sagebrush (5 to 9 in PZ)
Low Resilience and Resistance



1 Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens. Fire is rare in this system.

2a Sagebrush increases with time until co-dominant with the herbaceous understory.

2b Perennial grass and forbs becomedominant due to disturbances that decrease sagebrush. Fire is rare.

3a Sagebrush increases with time until dominant.

3b Perennial grass and forbs increase due to minor disturbances that decrease sagebrush.

T4 Frequent and severe grazing coupled with frequent brush management and/or drought results in dominance of grazing tolerant and sod-forming warm and cool season species. As bare ground increases, surface erosion (e.g., rills, sheet erosion) and pedestalled plants (especially bunchgrasses) result.

T5 Improper grazing, consisting of frequent and severe grazing without other disturbances such as fire or drought, results in dominance of sagebrush with excessive bare ground, resulting in altered hydrologic function and compromised soil stability.

T6 Annual invasives are introduced to the site through ground disturbing activity. Site is dominated by sprouting shrubs such as rabbitbrush and/or greasewood.

7a Sagebrush increases with time and removal of disturbances until dominant.

7b Perennial cool season sod-forming grasses and cactus increase due to disturbances that decrease sagebrush such as sagebrush treatment, drought, freezing, flooding, insects, disease, and pathogens.

T8 Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing by cattle and absences of sagebrush killing disturbances, resulting in altered biotic, hydrologic, and soil function. This state is at-risk of cheatgrass invasion.

T9 If a cheatgrass seed source is introduced, and catastrophic event occurs to kill perennial vegetation, such as drought followed by wet spring, cheatgrass can invade and dominate.

T10 A sagebrush killing event, such as fire and fire surrogates will dramatically increase cheatgrass while removing sagebrush from the system.

R11 A restoration treatment, including chemical treatment for cheatgrass and seeding (native or introduced mix), favorable climatic conditions (wet spring), rest from grazing during establishment, and a grazing system that allows for adequate rest and recovery of perennial forage species can restore a perennial grass community and eventually support an altered sagebrush community with invaders present. Sagebrush will not likely dominate in the foreseeable future. The Altered/Seeded State is possible from any state after a severe ground disturbing activity such as mineral extraction.

T12 A catastrophic event such as fire or drought, followed by a wet spring can result in a system dominated by annual invasive species.

13a Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory, but cheatgrass will be present. Introduced species are likely present if seeded during a restoration activity.

13b Perennial grass/annual and perennial forbs become dominant due to disturbances that decrease sagebrush. There will commonly be a temporary flush of annual invasives.

Strategies to Conserve Sagebrush Ecosystems and Sage-Grouse

Vegetation and fuels management projects are important for the conservation, maintenance, and restoration of sagebrush landscapes. Resilience and resistance concepts provide a science-based background that can inform strategic placement of fuels treatments, augment effective fire operations, and inform allocation of scarce assets during periods of heightened fire activity across the Interior West. Collectively, fuels management includes vegetation projects that mitigate wildfire risk, improve resilience to disturbance, and restore habitat, as well as habitat protection projects intended to protect intact sage-grouse habitat (fig. A7.1, A7.2). Mechanical treatments are typically applied to reduce fuel loading or to change species composition consistent with land management objectives. Prescribed burning is used to improve habitat conditions or create fuel conditions that reduce negative impacts from wildfire. Also, chemical and seeding treatments are conducted to reduce invasive plant species and to shift species composition to native or more fire resistant species.

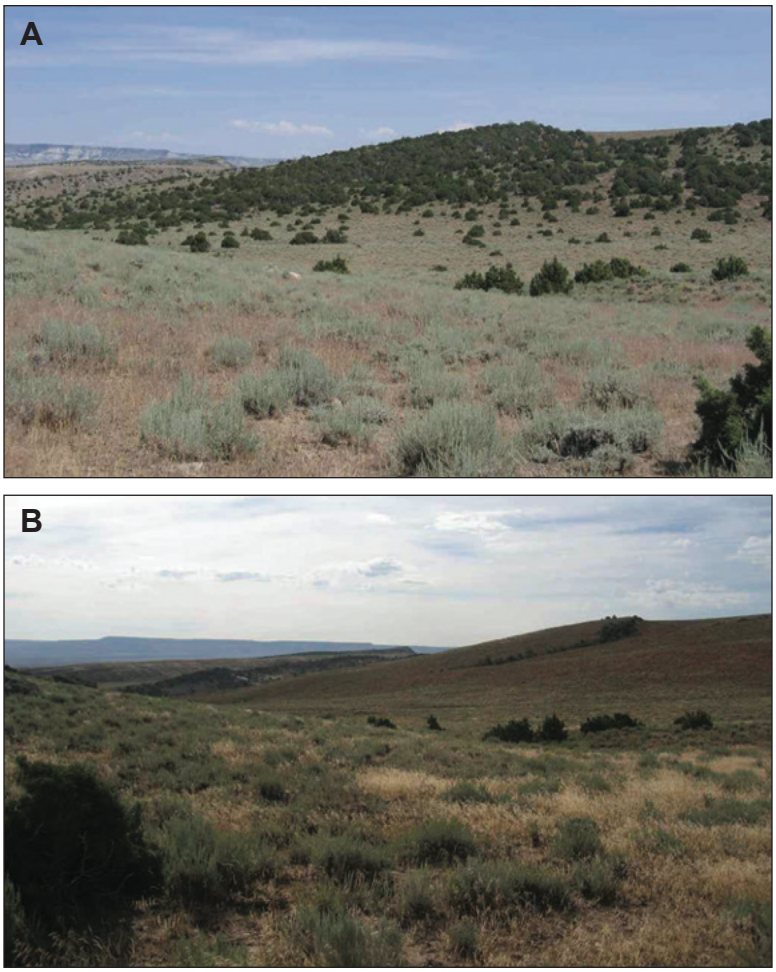
In fire operations, firefighter and public safety is the overriding objective in all decisions; land managers, however, also consider numerous other values at risk, including the wildland-urban interface, species habitats, and infrastructure when allocating assets and prioritizing efforts. In each case, managers are designing management activities that reflect the unique ecosystem responses that occur across environmental gradients. Resilience and resistance concepts are especially relevant for evaluating tradeoffs related to current ecological conditions, rates of recovery, and possible ecological consequences of different fire management activities. For example, prioritizing initial attack efforts based on ecological types and their resilience and resistance at fire locations is one application of resilience and resistance concepts. Also, fire prevention efforts can be focused on intact, high quality habitats with inherently low resilience and resistance where human ignitions have commonly occurred.

Fuels management projects are often applied on a landscape scale to (1) constrain or minimize fire spread; (2) alter species composition; (3) modify fire intensity, severity, or effects; (4) create fuel breaks or anchor points that augment fire management efforts; (5) improve wildlife habitat; (6) create resilient landscapes; and (7) restore habitats or vegetation conditions (see table 5). These activities are selectively used based on the projected ecosystem response, anticipated fire patterns, and probability of success. For example, in areas that are difficult to restore due to low to moderate resilience, fuel treatments can be placed to minimize fire spread and conserve sagebrush habitat. In cooler and moister areas with moderate to high resilience and resistance, mechanical or prescribed fire treatments may be appropriate to prevent conifer expansion and dominance.

Given projected climate change and longer fire seasons across the western United States, fuels management represents a proactive approach for modifying large fire trends and maintaining desired vegetation patterns. Fire operations and fuels management programs contribute to a strategic, landscape approach when coupled with data that illustrate the likelihood of fire occurrence, potential fire behavior, and risk assessments (Finney et al. 2010; Oregon Department of Forestry 2013). In tandem with resilience and resistance concepts, these data can further inform fire operations and fuels management decisions.



aLB(4tt —Common fuels management practices to improve sage-grouse habitat. Photos A and B show conifer mastication using a bobcat and bullhog. Photo C shows hand removal of conifers using a chainsaw. Photo D shows targeted prescribed burning in a mountain big sagebrush area exhibiting conifer expansion. Adjacent, intact sagebrush communities are intentionally avoided. Photos E and F show targeted prescribed burning of masticated and standing juniper fuels while intentionally avoiding sagebrush communities (Bureau of Land Management file photos).



aLB(4 t —Before (A) and after (B) photos of mechanical conifer removal within Greater sage-grouse habitat southeast of Lander, Wyoming. This project had the objectives of moderating fire behavior characteristics and improving Greater sage-grouse and mule deer habitat. Fuels managers have been successful in restoring Greater sage-grouse habitats through mechanical treatments that reduce conifer dominance (Bureau of Land Management file photos).

Fire managers and researchers are closely analyzing wildfire trends in the eastern range of GRSG and the entire range of GUSG. Recent fire history, climate trends, wildfire probability, and vegetation changes are key sources of data that are being used to develop proactive measures being implemented by the fire operations and fuels management programs. Concerns of fire and fuels managers in the eastern range include large fires in or adjacent to sage-grouse habitats, increases in woody plant expansion, and increases in the extent of nonnative annual grass populations. Currently there is little evidence of the same type of feedback cycle between wildfires, annual grasses, and larger fire size as exists in the western portion of the range (Taylor et al. 2014). Managers are aware of this potential, however, and are monitoring trends in fire size, postfire community composition, and rehabilitation success to detect the development of this type of cycle and adapt management to ensure positive future trends. Several large, severe fires have burned in sagebrush and grass ecosystems or sagebrush ecosystems exhibiting piñon and juniper expansion since 2000, including: Alkali, Colorado, (2014; 22,000 ac [8,903 ha]); Wolf Den,

Utah (2012; 19,865 ac [8,039 ha]); Cato, Wyoming (2012; 27,680 ac [11,202 ha]); Sheep Mountain, Wyoming (2000; 34,346 ac [13,899 ha]); and Wildhorse Basin, Wyoming (2000; 36,762 ac [14,877 ha]).

Proactive fuels management practices in the eastern range of GRSG differ from those in the western range. For example, roadside linear fuel breaks are seldom used in the eastern range, but are more commonly used in the western range. Conifer expansion in the western range is largely pinñon and juniper species; expanding conifers in the eastern range include limber pine (*Pinus flexilus*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*). In addition, successional advancement of mountain shrubs in Management Zone VII (e.g., gambel oak [*Quercus gambelii*], serviceberry [*Amelanchier* spp.], curlleaf mountain mahogany [*Cercocarpus ledifolius*], snowberry [*Symphoricarpos* spp.], and cliff fendlerbush [*Fendlera rupicola*]) into sagebrush communities are treated as a vegetation management issue.

Mechanical treatments of expanding conifers, which include mastication and chainsaw treatments, are increasingly used in the eastern range to retain sagebrush cover. Prescribed burning, a fuels management tool, is selectively applied in eastern range GRSG habitats, typically to: (1) reduce downed woody fuels resulting from mechanical treatments; (2) treat expanding conifers; (3) convert conifer woodlands to shrub-steppe; (4) reduce the dominance of mountain shrub communities to favor sagebrush; (5) create age class and structural diversity within sagebrush communities; and (6) restore riparian systems through multi-phased treatments. Managers are cognizant of the tradeoffs related to sagebrush removal through burning and apply this tool in consultation with wildlife managers and in consideration of site conditions. Additional fuels management practices in the eastern range include monitoring and treating areas with invasive annual grass populations with herbicides and seedings where insufficient perennial grasses and forbs exist for recovery, and installing fuels breaks, which can complement fire suppression effectiveness.

In the eastern range, cooperators such as rural, city, and State agencies contribute to GRSG conservation through their roles in both fire suppression and fuels management. Unlike areas in the western range where there are unprotected lands, in the eastern range, States and counties have jurisdictional responsibilities for wildfires on State and private lands. There are isolated, underprotected lands in the eastern range where opportunities exist to develop additional, non-Federal capacity, particularly by providing training and equipment, should Federal funding be made available.

The tools and data presented in this section can be used by fire and fuels managers, in cooperation with resource managers, to inform strategies for fire operations and fuels management related to suppression responses, treatment planning, and postfire management. Postfire rehabilitation in the eastern range is a cross-cutting effort involving disciplines such as range, wildlife, fire, and fuels management. Managers apply knowledge of seed zones, resilience and resistance, and ecological sites to inform rehabilitation strategies. The postfire emergency stabilization and rehabilitation handbook and manual (USDI BLM 2012) provide technical guidance on considerations in rehabilitation practices. The importance of GRSG and GUSG habitats is recognized in dispatch procedures and allocation of resources for wildfire incident management. These efforts align with the recommendations/guidance in the Final Report for the DOI Secretarial Order 3336 (USDI 2015).

Assessing the projected magnitude of climate change for a given area provides a basis for informed management into the future. The degree to which climate change and other stressors interact influences the approaches that can be taken to minimize losses. In those areas where climate change interactions are expected to be relatively small, and knowledge and capacity high, a logical approach might be to continue to use best management practices. In areas where the effects of climate change and its interactions with stressors are expected to be severe, our current suite of management actions may be ineffective.

Where climate change-stressor interactions are expected to be small, the logical approach is to use best management practices to build resilience to climate change into sagebrush ecosystems. Maintaining and restoring habitat, conservation actions to facilitate species of interest, and an increased emphasis on managing other stressors, such as nonnative invasive plants, improper grazing, and fire, are key components of building resilience.

As climate change progresses and temperatures increase, the frequency and magnitude of drought is expected to increase. Implementing measures to reduce the interacting negative effects of habitat loss and climate change and facilitate recovery from drought will become increasingly important. Drought adaptation measures may include changes in land uses such as a reduction in livestock stocking rates because plants that have been overgrazed or cropped too frequently are less able to recover after drought (Hart and Carpenter 2005). An increased emphasis on early detection and rapid response to address nonnative invasive plants may be needed as climate suitability for species like cheatgrass is likely to increase in many areas (Bradley et al. 2016). Also, habitat modifications such as creating and protecting migration corridors in fragmented landscapes may be necessary to facilitate persistence of sage-grouse and other species that use sagebrush habitats such as mule deer (Anderson and Jenkins 2006).

Drought adaptation may require modifying or delaying restoration practices during droughts. For example, it may be best to focus restoration efforts on removal of undesirable plants as opposed to planting treatments. In the West-Central Semiarid Prairies, efforts to restore native grassland may be more effective when crested wheatgrass control measures are implemented in drier years and native species are seeded in wetter years (Bakker et al. 2003). In the Cold Desert, juniper removal by mastication (shredding) can both decrease competition for water and enhance soil moisture beneath shredded debris benefitting herbaceous species (Young et al. 2013), potentially offsetting the effects of drought. If planting is deemed necessary during a drought year, a variety of strategies and techniques can be employed to increase the probability of successful plant establishment in the short term and species persistence in the long term (see review in Finch et al. 2016). For example, snow fences were constructed and arranged to maximize snow capture and increase sagebrush establishment on abandoned natural gas pads in the Wyoming Basin (David 2013). Stubble from winter-sown annual crops has been shown to capture snow and may benefit seedling establishment in the West-Central Semiarid Prairies (Greb 1980). Also, pitters and imprinters can be used to create micro-catchments in the soil that capture and concentrate water (Bainbridge 2007).

Regardless of the seeding or planting technique used, plant materials should be carefully selected to ensure that the species and ecotypes are adapted to both site conditions and drought and that they are resilient if drought is episodic or long-term climate change is projected. Transplanting has been found to be effective for establishing shrubs and forbs in water-limited environments, especially if transplants are hardened prior to planting and provided with supplementary water afterwards (Bainbridge 2007).

Current management strategies may be ineffective where the effects of climate change and its interactions with stressors are expected to be severe. In this case more proactive strategies for habitat management may be necessary to facilitate transition to a new site potential. Assisted migration, the purposeful movement of individuals or propagules of a species to facilitate or mimic natural range expansion or long distance gene flow within the current range, may become integral to conservation strategies as the rate of climate change increases (Havens et al. 2015). Assisted migration can encompass a broad range of goals, from minimizing loss of biodiversity to preventing extinction, and it can operate at a range of spatial scales, from local to continental (Williams and Dumroese 2013). Seed transfer guidelines can be used to determine transfer distances that avoid maladaptation (Johnson et al. 2004). These guidelines can be reprojected using models of expected future environmental conditions (Thomson et al. 2010) and will play an integral role in the planning of assisted migration efforts under climate change.

Management and research studies coupled with landscape monitoring can provide the basis for developing cost-effective and feasible management strategies for adapting to climate change. Carefully designed studies can increase our understanding of viable approaches for adaption measures such as appropriate grazing regimes for drought conditions, conservation actions to facilitate species persistence during climate warming, seeding and transplanting techniques during drought, and species and ecotypes for assisted migration. Monitoring to detect the rates and magnitudes of change occurring across the landscape can preemptively identify both populations and habitats that may suffer decline (Carwardine et al. 2011; Field et al. 2004). Monitoring can also identify potential new or novel combinations of species that constitute a functioning ecosystem under climate change. Increased understanding of both the changes occurring and viable strategies for addressing that change can reduce uncertainty and provide direction for proactive management strategies (Hobbs et al. 2009).



In accordance with Federal civil rights law and U.S. Department of Agriculture (USDA)
institutions participating in or administering USDA programs are prohibited from discrimi-
derived from a public assistance program, political beliefs, or reprisal or retaliation for prior

Persons with disabilities who require alternative means of communication for program information (e.g., Braille, large print, audiotape, American Sign Language, etc.) should contact

program.intake@usda.gov.

To learn more about RMRS publications or search our online titles:

www.fs.fed.us/rm/publications

www.treesearch.fs.fed.us

Ecosystems
https://doi.org/10.1007/s10021-018-0230-8
© 2018 Springer Science+Business Media, LLC, part of Springer Nature (outside the USA)

Fire and Grazing Influence Site Resistance to *Bromus tectorum* Through Their Effects on Shrub, Bunchgrass and Biocrust Communities in the Great Basin (USA)

Lea A. Condon[1,2]* and David A. Pyke[2]

[1]*Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, Oregon 97333, USA;* [2]*Present address: Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, Corvallis, Oregon 97331, USA*

Abstract

Shrubs, bunchgrasses and biological soil crusts (biocrusts) are believed to contribute to site resistance to plant invasions in the presence of cattle grazing. Although fire is a concomitant disturbance with grazing, little is known regarding their combined impacts on invasion resistance. We are the first to date to test the idea that biotic communities mediate the effects of disturbance on site resistance. We assessed cover of *Bromus tectorum*, shrubs, native bunchgrasses, lichens and mosses in 99 burned and unburned plots located on similar soils where fires occurred between 12 and 23 years before sampling. Structural equation modeling was used to test hypothesized relationships between environmental and disturbance characteristics, the biotic community and resistance to *B. tectorum* cover. Characteristics of fire and grazing did not directly relate to cover of *B. tectorum*. Relationships were mediated through shrub, bunchgrass and biocrust communities. Increased site resistance following fire was associated with higher bunchgrass cover and recovery of bunchgrasses and mosses with time since fire. Evidence of grazing was more pronounced on burned sites and was positively correlated with the cover of *B. tectorum*, indicating an interaction between fire and grazing that decreases site resistance. Lichen cover showed a weak, negative relationship with cover of *B. tectorum*. Fire reduced near-term site resistance to *B. tectorum* on actively grazed rangelands. Independent of fire, grazing impacts resulted in reduced site resistance to *B. tectorum*, suggesting that grazing management that enhances plant and biocrust communities will also enhance site resistance.

Key words: biological soil crusts; gap size; Great Basin; lichens; mosses; sagebrush ecosystem; shrub–steppe; structural equation model.

Received 19 September 2017; accepted 21 January 2018

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s10021-018-0230-8) contains supplementary material, which is available to authorized users.

Author Contributions LAC and DAP conceived the study, analyzed the data, and wrote the paper.

Data for this article can be found at https://doi.org/10.5066/F72Z14S7.

**Corresponding author; e-mail:* lcondon@usgs.gov

Published online: 28 February 2018

Introduction

Ecosystem responses to compound disturbances are of concern across biomes and continents as climate, land use, and fire interact (Westerling and others 2006). Shrub–steppe ecosystems (also known as temperate deserts and semi-deserts), where the primary land use is livestock grazing, make up 15% of Eurasia and 3% of North America (West 1983a). Grazing has likely reduced fire size in western Eurasia following millennia of livestock use with shifts in livestock types from grass-dependent to more browse-dependent animals as herbaceous vegetation has become limited (Breckle 1983; West 1983b). Unlike western Eurasia, the Great Basin of North America has only been grazed by livestock for less than 130 years. Over the last 80 years, increased livestock management in the Great Basin has led to improved herbaceous production and rangeland condition (Box 1990). Although these ecosystems have not and may never return to their pre-livestock-grazing condition, they do allow for the examination of impacts related to both fire and grazing on a system that is less altered by anthropogenic influences compared to similar ecosystems globally. When fire and grazing occur in the presence of invasive species, fire regimes can change and further promote invasive species (Rossiter and others 2003).

In Great Basin shrub–steppe ecosystems, fire and grazing are thought to regulate dominance of the exotic annual grass, *Bromus tectorum* L. (Pyke and others 2016), although they have rarely been examined simultaneously (Davies and others 2016). *Bromus tectorum* was introduced into the region from Eurasia in the late 1800 s and attained its current distribution by the 1930 s (Mack 1981). The invasion history of *B. tectorum* is long, as it is classified as an archaeophyte in Central Europe, having established there from its native steppe communities of southern Europe and the Middle East where it can dominate shrub–steppe ecosystems following excessive grazing (Terpó and others 1999; Kaczmarski 2000). Populations from Central Europe are known to exhibit reduced biomass and fewer inflorescences when situated with more native plant communities, particularly high cover of native bunchgrasses (Fenesi and others 2011). In the Great Basin, *B. tectorum* often creates a continuous fuel among perennial vegetation, where it dominates interspaces among vascular plants that were previously occupied by biological soil crusts (for example, lichens, mosses, and cyanobacteria on the soil surface), thus allowing fires to become more frequent than the time needed for many native perennials to reach reproductive maturity (Brooks and others 2004). Bradley and others (2017) estimate *B. tectorum* is at 15% or greater cover on almost one-third of the Great Basin (210,000 km^2) and that 10.7% of this area, over 22,000 km^2, burned between 2000 and 2014, demonstrating the extent of the grass–fire cycle in the region.

Biotic communities can limit the magnitude of invasions by exotic species (Levine and others 2004). We use the Great Basin sagebrush steppe as a model to understand potential mechanisms that lead to ecosystem resistance to *B. tectorum* in temperate shrub–steppe ecosystems. The Great Basin sagebrush steppe is a comparable ecosystem to those of Eurasia, containing many similar lifeforms (for example, perennial bunchgrasses, fire-intolerant shrubs, and biological soil crusts [lichens, mosses, and cyanobacteria on the soil surface hereafter called biocrusts]; Walter and Box 1983). Understanding the strength of interactions between biotic communities and site resistance to *B. tectorum* in the presence of disturbances such as fire and grazing is crucial to the management of sagebrush steppe ecosystems. Here we use ''resistance'' in the ecological sense as it is used by D'Antonio and others (2009) to mean the ''ability of a community to withstand encroachment by nonnative species.''

Our goal in this study is to provide a comprehensive understanding of the role of the biotic community: shrubs, native bunchgrasses, and biocrusts in maintaining site resistance to *B. tectorum* in the presence of both fire and grazing across the region. We build upon two models of site resistance to *B. tectorum,* one in the presence of fire (Condon and others 2011) and one in the presence of grazing (Reisner and others 2013), linking these models with the findings of many studies on interactions between biotic, environmental and disturbance indicators (Table 1). Resistance in these models depended on cover of perennial vegetation, cover of biocrusts, or the distance among perennial plants. Expanding upon these models, we characterize fire and grazing with multiple factors that could be employed by land managers to predict and possibly facilitate site resistance (grazing animal stocking levels, fire severity, extent of fire, and time since fire). Additionally, we anticipated an interaction between fire and grazing, since cattle preferably use areas with light to moderate burn severity over unburned areas (Clark and others 2014). We expected that biocrusts would be more sensitive to disturbance, particularly grazing, compared to native bunchgrasses. In areas surrounding the Great Basin, results from surveys inside and

Table 1. Components of Hypotheses Represented by Initial Conceptual Model (Figure S1)

	Site resistance	
Abiotic factors		
HLE → + *Bromus*	↓	Increases in heat load result in reduced site resistance to *Bromus tectorum* L. (Chambers and others 2007; Condon and others 2011)
HLE → − grass cover	↓	Increases in heat load result in decreased productivity of bunchgrasses (Davies and others 2007)[1]
SPP → + bare ground	↓	Increased sand content is associated with increases in bare ground (BG) and *B. tectorum* establishment[1]
BG → + *Bromus*	↓	Safe sites in the form of bare ground (BG) increase establishment rates of *B. tectorum* (Fowler 1988)[1]
SPP → + *Bromus*	↓	Soils with deeper, coarser textures are associated with increased cover of *B. tectorum* (Stewart and Hull 1949)[1]
SPP → ± grass comp	↓ ↑	Increases in sand content are associated with different compositions of native bunchgrasses[1]
Grazing impacts		
Grazing → − biocrusts	↓	Grazing results in trampling of biocrusts and increases safe sites for establishment of *B. tectorum* (Ponzetti and others 2007)[1]
Grazing → ± *Bromus*	↓ ↑	Grazing results in a decrease in cover of *B. tectorum* by herbivory (Hempy-Mayer and Pyke 2009), an increase through propagule pressure via animal mediated seed dispersal (Schiffman 1997) or no direct effect in some areas[1]
Grazing → + gaps	↓	Increases in grazing intensity relate to positive increases in community gap structure (Condon and Pyke 2016)[1]
Grazing → − grass cover	↓	Cattle grazing decreases the cover of native bunchgrasses (Briske and Richards 1995)[1]
Grazing → ± grass comp	↓ ↑	Cattle grazing selects for a composition of native bunchgrasses that are more grazing-resistant (Briske and Richards 1995)[1]
Fire impacts		
Fire → − shrubs → + gaps Fire → − grass cover → + gaps Fire → − lichens/moss → + gaps Gaps → + *Bromus*	↓	By reducing understory species (shrubs, bunchgrasses, mosses, and lichens), fire increases gap community structure and temporarily increases safe sites for *B. tectorum* (Johansen and others 1984; Chambers and others 2007; Pyke and others 2015). Understory species recover with increasing time since fire and take longer to recover into fires of greater extent (Johansen and others 1984; Condon and Weisberg 2016)
Fire → + *Bromus*	↓	Fire may result in a direct increase in *B. tectorum* (Miller and others 2013)
Fire → + grass cover	↑	Fire may increase cover of native bunchgrasses after short-term reductions in cover (Cooper and others 2011)
Biotic interactions		
Grass cover → − *Bromus*	↑	Increased native bunchgrass cover results in fewer safe sites for establishment and reduced cover of *B. tectorum* (Chambers and others 2007; Condon and others 2011)
Shrubs → − *Bromus* Moss → − *Bromus* Lichen → − *Bromus*	↑	Cover of *B. tectorum* is reduced in the presence of shrubs, mosses, and lichens (Serpe and others 2006, 2008; Reisner and others 2015)
Moss → + grass cover Lichen → + grass cover	↑	The establishment, survival, nutrient status, and water relations of native bunchgrasses are influenced by mosses and lichens (Prasse and Bornkamm 2000; Harper and Belnap 2001)
Grass comp → ± gaps	↓ ↑	Native bunchgrass composition influences the community gap structure with different life-forms (James and others 2008)[1]
Bunchgrass → − gaps	↑	Increased cover of native bunchgrasses reduces the community gap structure (Herrick and others 2005)[1]
Gaps → + bare ground Bare ground → + *Bromus* Gaps → + *Bromus*	↓	Increases in the community gap structure among perennial vegetation increases the number of safe sites for *B. tectorum* as well as the cover of *B. tectorum* as a result of increased resource availability (James and others 2008)[1]
Interaction between fire and grazing		
Fire → + grazing	↓	Fire promotes grazing as cattle are more likely to use burned sites (Clark and others 2014)

HLE, heat load index; SPP, soil physical properties.
[1]*Demonstrated in Reisner and others 2013 and tested region-wide in this study.*

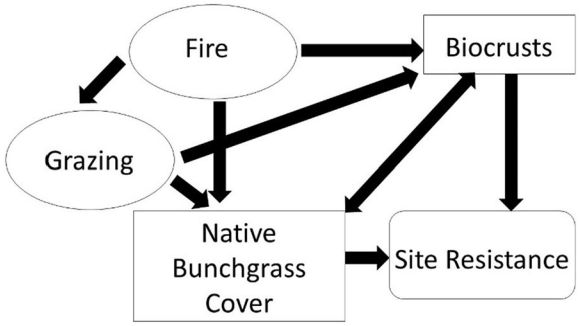


Figure 1. Meta-model representing the influence of biocrusts and native bunchgrass cover on site resistance (*Bromus tectorum* L. cover) in the presence of fire and grazing. Disturbance variables are presented in ovals. Biotic factors are presented in rectangles. Site resistance (*Bromus tectorum* L. cover) is presented in a rounded rectangle. Only the presence and not the strength of these relationships is hypothesized in the model.

outside of livestock exclosures have demonstrated differences in biocrust abundance (Kleiner and Harper 1972) and community composition (Ponzetti and McCune 2001), indicating that some biocrusts are sensitive to livestock presence. In contrast, biocrust community composition following fire was similar to unburned sites when *B. tectorum* cover was low (less than 12% and one-third the cover of perennial grasses) (Bowker and others 2004). Similarly, cover of native bunchgrasses is reduced and composition is altered following sustained grazing by cattle (Briske and Richards 1995), and this in turn may increase the spatial distances among perennial grasses (Reisner and others 2013). Cover of bunchgrasses is temporarily reduced, but often increases following fire (Cooper and others 2011). Grasses located under shrubs will likely die because of the increased temperature of the burning woody fuel (Boyd and others 2015) and thus may increase gaps among perennial plants. We expected to observe interactions between biocrusts and native bunchgrasses since biocrusts have been shown to facilitate the establishment, survival, nutrient status, and water relations of native bunchgrasses (Prasse and Bornkamm 2000; Harper and Belnap 2001). These relationships are conceptually presented in a meta-model (Figure 1).

Hypothesized relationships between fire and grazing on impacts to lichens, mosses, shrubs, and native bunchgrasses (cover and composition) are presented using a system-level approach due to the large number of potential interconnections among biotic, environmental, and disturbance indicators (Table 1, Appendix 1 Figure S1). At the regional scale, we expected sites to vary in their inherent resistance to invasion by *B. tectorum* based on the environmental tolerances of *B. tectorum* (Chambers and others 2007; Condon and others 2011; Chambers and others 2014). Our area of inference is the northern Great Basin with a wider range of annual precipitation than considered by previous models (Condon and others 2011; Reisner and others 2013). In sum, we hypothesized that single fires lead to temporary declines in site resistance, but that decreases in grazing intensity by livestock, either before or after the fire, would lead to increases in site resistance, meditated through increases in the cover of native bunchgrasses and biological soil crusts and through reductions in the distances among perennial plants.

Materials and Methods

Area of Inference and Study Sites

The area of inference consists of big sagebrush (subspecies of *Artemisia tridentata*, family Asteraceae) ecosystems on loamy-textured surface soils, managed by the Bureau of Land Management (BLM) within southeastern Oregon, southwestern to southcentral Idaho, northern Nevada, and western Utah. Wyoming big sagebrush and mountain big sagebrush subspecies of sagebrush (*A. t.* ssp. *wyomingensis* Beetle and Young and *A. t.* ssp. *vaseyana* (Rydb.) Beetle) were lumped in this study. Common native perennial bunchgrasses encountered include *Achnatherum hymenoides* (Roem. and Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezy, *Poa secunda* J. Presl, and *Pseudoroegneria spicata* (Pursch) Á. Löve. The region spans a gradient of increasing productivity from south to north and from lower to higher elevations, covering seven Major Land Resource Areas (similar to ecoregions; USDA NRCS 2006, Figure 2). Annual average precipitation across the region ranged between 158 and 419 mm (West 1983c), while the sites that we sampled ranged from 127 to 556 mm of precipitation during the first three years following fires. Landscapes represented in our sample have likely experienced regular grazing for nearly 100 years. Since the 1970s, some grazing allotments have changed from season-long or continuous year-round livestock grazing to deferred or rest-rotation grazing systems to provide annual changes in grazing seasons and periods of rest (no grazing) (Howery and others 2009).

Fifteen fire locations included in this study were a subset from Knutson and others (2014). Each location was within a single grazing allotment or pasture within an allotment (Figure 2) and con-

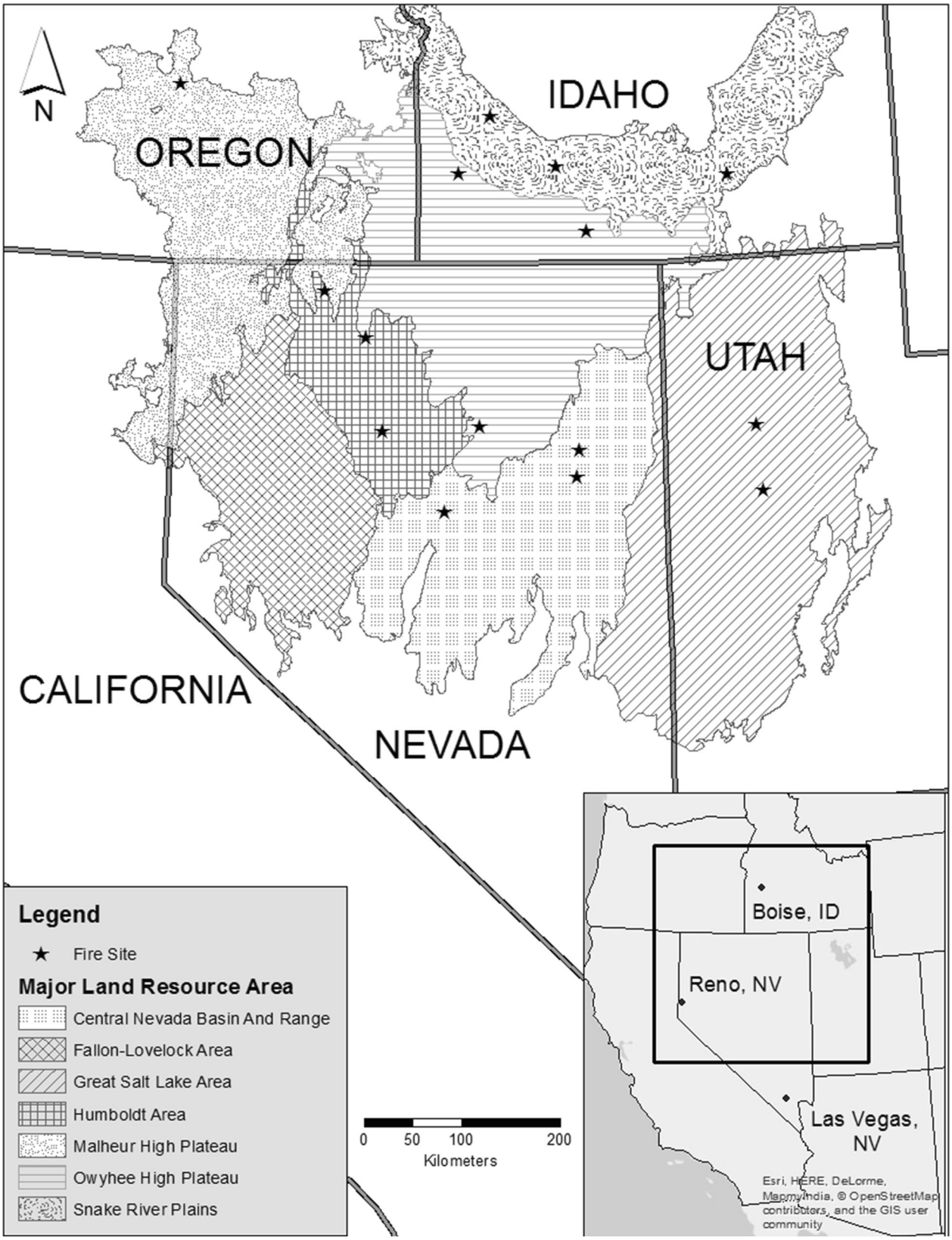


Figure 2. The locations of the fifteen fires surveyed relative to the major land resource areas across the Great Basin, USA.

Table 2. Variables Considered in Site Selection from Knutson and others 2014[1]

Description	Units	Mean (S.D.)	Range
Average precipitation[1] (PRISM 2010)			
Average precipitation is given for each of the three water years following the fire as modeled by PRISM	Mm	WY 1-256 (54) WY 2-274 (74) WY 3-300 (101)	WY 1-179–373 WY 2-168–437 WY 3-155–556
Fire severity[1] (MTBS 2012)			
Fire severity was estimated with dNBR. Sites were selected to cover a range of fire severities. Plots were classified according to their dominant fire severity	N/A	N/A	Unburned—51 p Low severity—29 p Moderate severity—16 p High severity—3 p
Season of fire[1] (MTBS 2012)			
Julian date of ignition	N/A	222 August 10 (24.5)	160–259 (June 9–Sept 16)
Time since fire[1] (Pilliod and Welty 2013)			
The number of years between the fire and the 2012–13 sampling date	Years	16 (3.8)	12–23 (1990–2001)
Total area burned[1] (Pilliod and Welty 2013)			
The area inside the fire perimeter measured in ArcMap	Hectares	6013.9 (10,269.3)	540.7–42,920.6
Average and standard deviation in the gap among perennial plants (field measured, Knutson and others 2014)			
Standard deviation of the average (avg) gap among perennial plants along the 50-m transects at each plot	Cm	Avg gap-230.1 (553.7) SD of avg gap-199.5 (297.8)	Average-36.3–5000 SD-0–1962
Dung density[1] (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx)			
Dung from cattle per meter squared counted in shrub belt transects.	#/m^2	5 (5)	0–25
Distance from water (derived from GIS with http://nhd.usgs.gov and 1-m resolution NAIP imagery)			
Mapped and measured with NAIP and National Hydrography Dataset	Meters	1915.1 (1294.2)	144.3–5802.8
Active AUMs (Rangeland Administration System http://www.blm.gov/ras/)			
Active AUMs as of September 15, 2015	AUMs	5320.7 (4555.9)	0–13,326
Suspended AUMs (Rangeland Administration System http://www.blm.gov/ras/)			
Suspended AUMs as of September 15, 2015	AUMs	1297.6 (2269.6)	0–7473
Permitted AUMS			
Permitted AUMs as of September 15, 2015 (estimated capacity)	AUMs	6618.2 (5858.8)	0–15,174

All listed variables were considered in analysis. Average values and (standard deviations) are shown. Headings are variables (sources of information).
AUMs, animal unit months; dNBR, differenced normalized burn ratio; MTBS, monitoring trends and burn severity database; p, plots; WY, water year.
[1]*Sites were selected to represent the range of values.*

sisted of at least three plots each within: (1) a wildfire and not reseeded after the fire; and (2) an unburned area that surrounded the burned area, but on the same ecological site as burned plots (that is, land potential; USDA NRCS 2003). Plots were randomly placed within similar soil map unit components within the fire and were verified in the field to insure the same ecological site. Fire locations were selected to cover a broad range of predictor variable values, which included average

precipitation for each of three years following the fire, elevation, fire severity, time since fire, season of ignition, total acres burned, and grazing intensity represented by cattle dung density (dung density), Table 2). We have described fire locations in regard to both cover of *B. tectorum* found in burned and unburned plots and site resistance as determined by soil temperature and moisture regimes (Chambers and others 2014, Table 3), demonstrating that these sites are within the range of *B. tectorum*. Further description of all locations can be found in Knutson and others 2014. Plots (total of 99 plots; one fire location had six unburned plots and three burned plots, and another fire had a total of six unburned plots and six burned plots) were circular with three, 50-m transects beginning 5 m from a central point and radiating from that point every 120° (Herrick and others 2005). Shrub density by species was counted in 2-m or 6-m (burned or unburned plots) by 50-m belt transects (Knutson and others 2014). In 2012 and 2013, we measured canopy cover of biocrusts (mosses and lichens) and vascular plant life-forms (shrubs, native bunchgrass, and annual grasses (exclusively *B. tectorum*)). Cover was estimated visually (to the nearest 1%) within 0.25-m^2 square quadrats located at 10-m intervals along each transect for a total of 15 quadrats per plot. Factors that we expected to affect site resistance to *B. tectorum* (quantified as cover of *B. tectorum*) were measured at scales that matched the scale of process. For example, grazing is measured at a coarse scale (dung density within belt transects) and cover of biocrusts is measured at a fine scale (canopy cover in 0.25-m^2 square quadrats).

Characterization of Fire

For each fire, we included characteristics that are typically used to define fire regimes: severity, extent (area burned), and season of fire (Sugihara and others 2006, Table 1) and we added time since fire. Frequency of fire was not addressed because we selected sites that had burned only once since 1970 (Knutson and others 2014). Fire severity was represented by shrub cover lost to fire, which was more plot specific, compared to what was detected with remote sensing (Monitoring Trends in Burn Severity [MTBS] 2012). Fire extent was calculated in ArcMap 10.2 (ESRI 2013), and season of fire was reported from MTBS (2012, Table 1).

Characterization of Livestock Grazing

Characterizing cattle use on public lands is difficult in the Great Basin because monitoring data are often of different data types among allotments or management units (Veblen and others 2014). We examined several indicators of grazing intensity that were measured consistently and may relate to site resistance across the region. Using a piosphere approach, increasing distance to water, including springs, seeps, wells, and associated water troughs, was used as a proxy for declining grazing intensity (Andrew and Lange 1986; Landsburg and others

Table 3. Fire Names (Locations) and Fire Codes Summarized by Both Range in Cover of *Bromus tectorum* and Associated Resistance and Resilience Class Based on Soil Temperature and Moisture Regimes

Fire name, fire code	*Bromus tectorum* cover		Resistance and resilience class
	Burned plots	Unburned plots	
Castle Creek, F052	2–5 (3.0)	0–8 (4.0)	High
Pigtail Butte, F074	4–7 (5.7)	0 (0)	Low
RRMP, F116	3–11 (6.7)	13–19 (15.0)	Low
Wapi, F480	3–5 (4)	2–8 (4.3)	Low
Frenchie Flat, J194	11–15 (13.3)	2–10 (5.3)	Low
Junction, J458	13–15 (14)	5–15 (11.3)	Low
Trail Canyon, K909	14–15 (14.7)	3–10 (7)	Low
Butte, K267	10–15 (12.3)	0–2 (1.3)	Low
Cinder Butte, N567	7–9 (8)	6–14 (11)	Moderate
Eight Mile, Q161	15–16 (15.3)	10–14 (12)	Low
Keg Mountain, Q989	14–15 (14.7)	5–8 (6.3)	Low
Rabbit, X075	1–13 (6.3)	0 (0)	Low
Buffalo, X393	0–4 (2)	0–6 (1.7)	Low
King, X465	14–15 (14.3)	10–15 (13)	Low
East Slick, Z269	15–16 (15.3)	13–15 (14.3)	Low

Average cover on burned and unburned plots is shown in parentheses.

1997). Distance to the closest single water source was measured in ArcMap 10.2 (ESRI 2013) using a combination of 1-m resolution images from the National Agriculture Imagery Program and the National Hydrography Dataset (accessed February 10, 2016; http://nhd.usgs.gov, Table 1). A second measure of grazing intensity on site resistance was gap size (distance) among perennial vegetation (Reisner and others 2013; Condon and Pyke 2016). We used the standard deviation of the average gap size among perennial plants because this estimate of variance took into account site conditions and showed a stronger correlation with *B. tectorum* cover than average gap size. The standard deviation of the average gap size among perennial plants has a Pearson's correlation of 0.76 with the variable used by Reisner and others, percent of the line covered by gaps greater than 200 cm. A third measure, dung density, came from the Knutson and others (2014) dataset (sagemap.wr.usgs.gov/ESR_Chrono.aspx, Table 1).

We quantified current and historic grazing intensity with records provided by the BLM Rangeland Administration System (RAS 2015; http.www.blm.gov/ras/, accessed September 15, 2015). RAS data have recently been used to examine landscape-level cattle impacts on plant productivity and sage grouse population trends (Monroe and others 2017) and provides numbers of active use (synonymous with billed use, the amount of forage that livestock will likely use during the grazing period) and permitted use (maximum level of forage in the allotment that a livestock can use) in animal unit months (AUMs) per grazing allotment. AUMs are an estimate of the amount of forage needed to sustain a standard animal unit (for example, a 454-kg cow with a suckling calf for 1 month) onsite that can be translated into the number of animals the site can feed for a set time (Ruyle and Ogen 1993). RAS also reports the number of suspended AUMs, which is the number of AUMs removed from use that are not likely to be replaced. This should not be confused with AUMs that are temporarily suspended due to drought. Suspended AUMs can be viewed as an indicator that past livestock stocking levels were not meeting management objectives (vegetation or soil) and a long-term (quasi-permanent) AUM suspension was deemed appropriate to halt further decline in rangeland condition (Ruyle and Ogen 1993).

For each allotment, we created indices of past (suspended AUMs) and currently active (billed AUMs) grazing and divided them by the number permitted to standardize for differences in the allotment sizes. BLM grazing records immediately before and after each fire were not accessible for all sites. We used records that were available as of September 15, 2015, from the RAS. According to BLM staff (Lynnda Jackson, personal communication, September 9, 2015), AUMs do not change much making these records an acceptable substitute for pre- and post-fire livestock use. Out of a total of 15 grazing allotments that included all plots in this study, all but one site was reported as having active AUMs and 7 sites had suspended AUMs. Common federal practice at the time of these fires was that livestock grazing be halted for a minimum of two growing seasons following fires and then reinstated (Clark and others 2014), although some offices currently require that recovery objectives be met based on vegetation and soil factors before grazing resumes (Bureau of Land Management 2007).

Data Analysis

Structural equation modeling (SEM) was implemented with AMOS version 23.0.0 (Arbuckle 2014) and was used to evaluate hypothesized effects of fire, grazing, and the interconnections between biocrusts and vegetation with subsequent effects on cover of *B. tectorum* based on an a priori conceptual model (Appendix 1 Figure S1). Specific pathways among environmental factors, grazing impacts, fire impacts, and biotic interactions are described and justified in Table 1. The use of SEM allowed us to assess effects of fire versus grazing on the cover of biocrusts and native bunchgrasses as they relate to site resistance to *B. tectorum*. As opposed to other multivariate analyses, SEM provides confirmatory tests and is more suitable for evaluation of multivariate hypotheses (Grace 2006). Response variables are those that are at the terminal end of a pathway (Appendix 1 Figure S1). Model specification, evaluation, and interpretation followed the guidelines in Grace and others (2012). Global estimation and evaluation methods were chosen for this application. Pathways are summarized by linear relationships based on the relatively short amount of time since fire of 12–23 years.

Non-metric multidimensional scaling (NMS) ordination axes of bunchgrass species cover were used as an indicator of native bunchgrass community composition (McCune and Grace 2002). All variables were *z*-transformed (the mean was subtracted from each value, and the resulting difference was divided by the standard deviation of the variable), with the exception of the ''burned'' variable, which was binary (burned or not burned) and so not standardized.

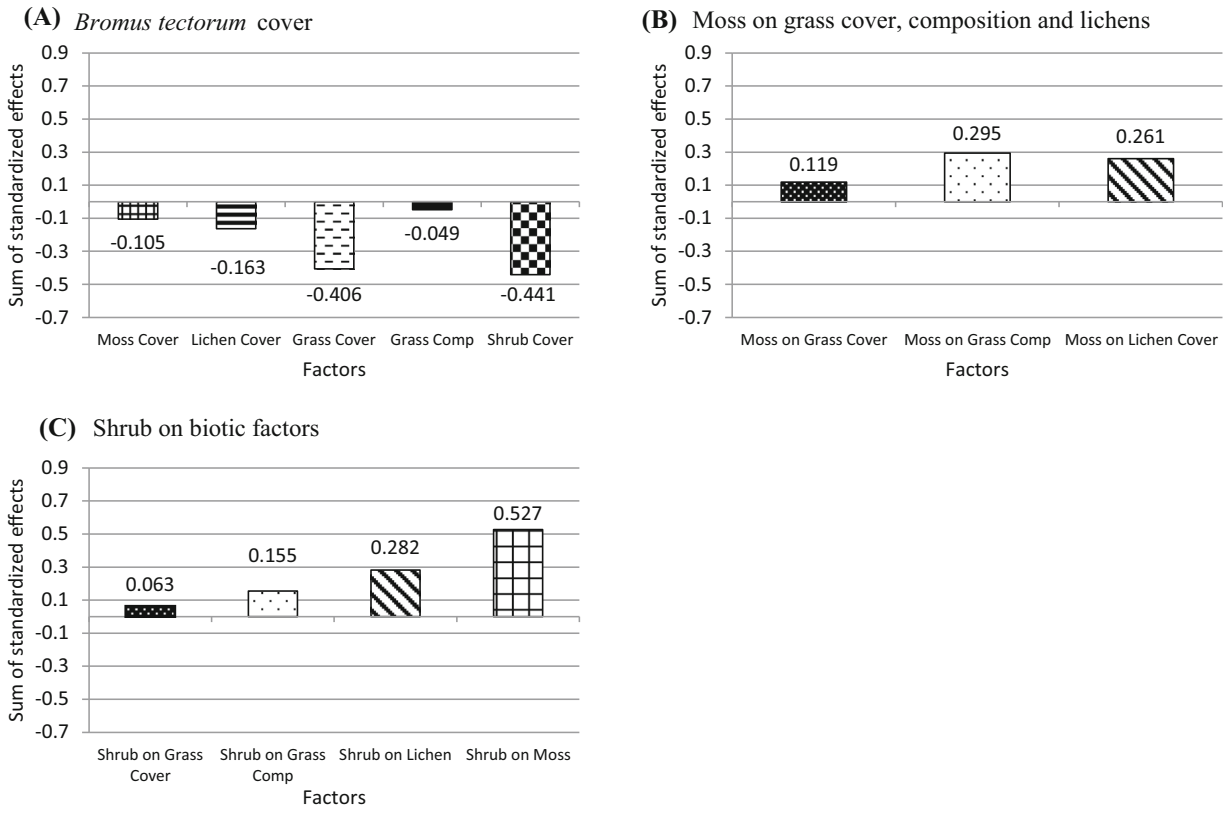


Figure 3. Sum of the standardized effects of **A** biotic factors on *Bromus tectorum,* **B** moss cover on native bunchgrass cover, composition, and lichens, **C** shrub cover on native bunchgrass cover, composition, lichens, and mosses. Abbreviations for significant factors are as follows: grass cover–native bunchgrass cover, grass comp–native bunchgrass composition *Y*-axis is unitless. Pathways used to calculate these effects are presented in Figure S3.

We included all resulting pathways from Reisner and others (2013) in our a priori conceptual model. The relationship between perennial herbaceous cover and cheatgrass in the presence of fire was established in Condon and others (2011), but here we replace perennial herbaceous cover with native bunchgrass cover so as to be consistent with Reisner and others (2013). Hypothesized pathways that were added to characterize disturbances were first visually examined in scatterplots for relationships among variables of interest before being added to our conceptual model. Season of fire, as represented by the Julian date of ignition (Table 1), did not show a relationship with biocrust or bunchgrass recovery and so it was not included in our a priori model. Although fire severity as calculated by MTBS was included in our selection of surveyed sites, the ecologically meaningful metrics do not always relate well to MTBS (Table 1, Kolden and others 2015). Instead, we used the amount of shrub cover lost to fire to represent fire severity, which showed stronger relationships in the model compared with fire severity from MTBS. Other hypothesized pathways were as described above (Table 1, Figure S1). In an effort to achieve parsimony, pathways were only kept in the model if the associated p value was less than 0.1. Model fit was evaluated with both a Chi-squared test and a root-mean-squared error of approximation (RMSEA). A RMSEA takes into account the sample size and the number of pathways evaluated. A RMSEA that includes zero and an insignificant Chi-squared test indicates that the model fits the data well. Sum of standardized effects were calculated for factors of interest following methods described in Grace (2006).

Results

A model only including significant pathways showed a reasonable fit to the data (RMSEA 0.000, $X^2 = 77.5$, $p = 0.309$, $df = 72$). Neither fire nor grazing produced direct effects on *B. tectorum* cover, but their impacts were expressed indirectly through impacts on other biotic factors (Figure S2). The model provides evidence that increases in cover of

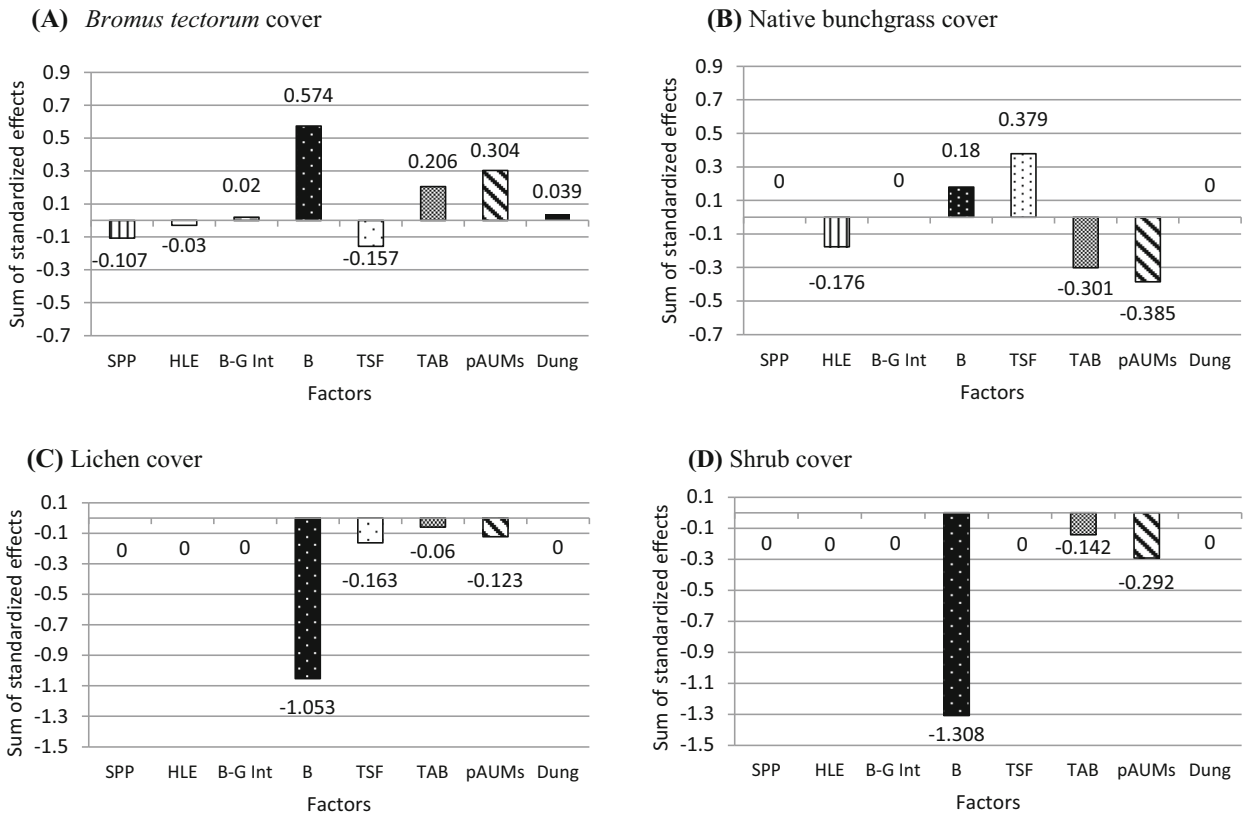


Figure 4. Sum of the standardized effects of fire, grazing, and environmental factors on **A** *Bromus tectorum* cover, **B** native bunchgrass cover, **C** lichen cover and **D** shrub cover. Abbreviations for significant factors are as follows: SPP—soil physical properties, HLE—heat load exposure, B—burned, B–G Int—burned area–grazing interaction, TSF—time since fire, TAB—total area burned, pAUMs—proportion of suspended AUMs. *Y*-axis is unit less. Pathways used to calculate these effects are presented in Figure S4. *Bromus* is also affected by gaps among perennials with a standardized effect of 0.204.

bare ground, shrubs, native bunchgrasses, and lichens along with decreases in the variation in sizes of gaps among perennial plants are directly associated with reduced cover of *B. tectorum*. Given that cover of *B. tectorum* was largely driven by the response of the biotic community to disturbance, we present our results in the following order: relationships among biotic factors including *B. tectorum*, relationships between biotic factors and disturbance, and relationships between biotic and abiotic factors. Additionally, pathways included in each sum of standardized effects are outlined in Figure S3 for Figure 3 and Figure S4 for Figure 4 for repeatability.

Biotic factors reduced cover of *B. tectorum*. Standardized effects of shrub, native bunchgrass, lichen, and moss cover, and to a lesser degree, native bunchgrass composition were all associated with reduced cover of *B. tectorum* (Figure 3). Increased moss cover was associated with increased lichen cover, native bunchgrass cover, and composition (Figure 3). Increased shrub cover was directly associated with reduced cover of *B. tectorum* and increased lichen and moss cover. Increased shrub cover was indirectly associated with increased native bunchgrass cover and composition. Increased variation in the size of gaps among perennials is a measure of disturbance effects on the biotic community, which had a subsequent direct effect on facilitating cover of *B. tectorum* (Figure 4, Figure S2).

Fire and grazing affected biotic factors (Figure 4). Cover of *B. tectorum* increased following fire and with greater total area burned (Figure 4a). Cover of *B. tectorum* decreased with increasing time since fire. Active AUMs did not have a role in the model explaining biotic response, but increased historical grazing pressure represented by suspended AUMs, and to a lesser degree, increases in dung density increased *B. tectorum* cover. Further increases in grazing pressure were observed on burned sites, leading to further increases in cover of *B. tectorum* (burned area–grazing interaction, Figure 4a).

Native bunchgrass cover increased with fire and time since fire although reductions in cover were observed on sites with greater amounts of heat load, of total area burned, and of historical grazing pressure as represented by suspended AUMs (Figure 4b). Lichens were observed to be sensitive to fire, time since fire, total area burned, and historical grazing pressure as represented by suspended AUMs (Figure 4c). Shrub cover was reduced in both the presence of fire and on sites with greater amounts of total area burned (Figure 4d). Additional reductions in shrub cover were seen on sites with increased grazing pressure as represented by suspended AUMs.

Environmental factors of soil physical properties and heat load content also contributed to the explanation for *B. tectorum* cover. Increases in both soil physical properties (sand content) and heat load index were associated with reduced cover of *B. tectorum* (Figure 4a). In addition, increases in heat load index demonstrated reduced cover of native bunchgrasses on warmer and drier sites (Figure 4b).

Discussion

We are the first to quantify that site resistance to *B. tectorum* across the sagebrush steppe of the Great Basin is mediated through changes in the biotic community and those changes are driven by fire and livestock grazing. None of our studied disturbance factors had direct impacts on ecosystem resistance to *B. tectorum*, but rather they negatively impacted other biotic factors that in turn reduced site resistance. Factors relating to reduced *B. tectorum* cover were high cover of shrubs, perennial bunchgrasses, mosses, lichens, and bare ground and low variation in gap distances among perennial plants supporting previous models (Condon and others 2011; Reisner and others 2013) and studies (Chambers and others 2007). We had hypothesized that the proportion of active AUMs, representing grazing disturbance, and that the three factors representing fire disturbance: burning, time since fire, and acres burned, would be directly related to *B. tectorum* cover. However, none of these relationships were supported by the model. In addition, the sign of the relationship between cover of bare ground and *B. tectorum* cover in our model was reversed from that seen by Reisner and others (2013), but we believe differences in study designs may explain these opposing results.

Our study did not attempt to find locations within 100 m of livestock water points to describe conditions of areas with extreme livestock use (Reisner and others 2013). We accepted whatever distance occurred, and since more lands within the Great Basin are beyond 100 m from water, we were less likely to sample highly trampled lands with sustained overuse by livestock. The highly trampled areas near water in Reisner and others (2013) had both high *B. tectorum* cover and high cover of disturbed bare ground. Livestock hoof action likely broke up biocrusts, and killed perennial plants, while also working *B. tectorum* seed into the soil providing safe sites for establishment. Tolerance to grazing likely allowed *B. tectorum* to maintain high cover each year (Pyke 1987; Hempy-Mayer and Pyke 2009). In contrast, higher cover of bare ground in our study was associated with areas having larger distances from water and more native bunchgrass cover. These are likely locations where perennial plants and their roots dominate interspaces (Aguiar and Sala 1999; Reisner and others 2015) making it more difficult for *B. tectorum* to establish and produce high cover or large populations (Reichenberger and Pyke 1990).

Shrub and bunchgrass cover were the two most important biotic factors relating to site resistance, with direct and nearly equal negative relationships on *B. tectorum* cover. Increases in shrub cover facilitated increases in cover and composition of native bunchgrasses, and to a greater degree, increases in cover of lichens and mosses. Mosses facilitated both native bunchgrasses and lichens. These relationships were observed over the complete range of precipitation and temperature gradients present across the Great Basin.

Site resistance was also directly related to low variation in gap distances among perennials and lichen cover on *B. tectorum* cover. Gap variation was reduced when cover and composition of native bunchgrasses increased, likely due to having fewer long gaps and more short gaps among perennials, which is consistent with Reisner and others (2013). Although low variation could result from a large number of long gaps among perennial plants, only one plot fit this scenario of low perennial gap variation with high cheatgrass cover.

Abiotic factors resulted in some unexpected relationships, likely due to the regional scope of our study compared to both Condon and others (2011) and Reisner and others (2013). The positive relationship between high sand and bare ground cover was anticipated, but the positive relationship between heat load and bare ground was not hypothesized largely because it was not a significant factor in the model by Reisner and others (2013). However, both Condon and others (2011) and Reisner and others (2015) did find that warmer

and drier sites are more prone to *B. tectorum* invasion which our model supports. Simultaneously, the idea that more arid sites experienced greater increases in gaps among perennial plants fits within the concepts of resistance and resilience, under which, arid sites are more susceptible to invasion by *B. tectorum* following disturbance (Chambers and others 2014).

When perennial plants and biocrusts are intact, sites are resistant to *B. tectorum* and the subsequent creation of continuous fuels (Condon and others 2011; Reisner and others 2013). When *B. tectorum* is present in the ecosystem, fuels and subsequent fires are likely to be continuous and of larger extent. When grazing is light, perennial grasses remain in the interspaces (Reisner and others 2015) where they are more likely to survive fire. The acute disturbance of fire was strongly associated with reduced cover of shrubs, largely the fire-intolerant *A. tridentata,* and of biocrusts, leaving a void for increases in cover of *B. tectorum*. Large fires reduced bunchgrass cover and may relate to changes in fire behavior (for example, higher fire intensity producing lethal temperatures for bunchgrasses), but the mere fact that a fire burned the area tended to favor bunchgrass cover. In addition, some recovery of site resistance was observed with increasing time since fire of 12–23 years. Fire also had the biggest impact on increasing gap distances among perennials and adding to a net increase in *B. tectorum* cover following fire, likely due to the removal of shrubs (Pyke and others 2014). Native perennial grasslands with scattered sagebrush are thought to be maintained by fire (Wright and others 1979), which corroborates our finding of a positive effect of fire on bunchgrass cover. Recovery of shrubs following fire in the Great Basin is slow and patchy (Nelson and others 2014; Condon and Weisberg 2016) corroborating our observed lack of shrub recovery.

We expected that the effect of fire on native herbaceous flora would be temporary. Bunchgrasses and mosses increased in cover with increasing time since fire and were associated with decreased cover of *B. tectorum*. However, lichens did not increase with increasing time since fire. Bowker and others (2004) observed no significant differences in species composition of mosses or lichens following fire on sites that were ungrazed by livestock for 20 years in the Columbia Basin. Their burned locations tended to have lower mean cover on burned versus unburned areas. Our locations were grazed both before and shortly after the fires.

Significant factors in our study that characterized relationships between grazing intensity and vegetation relating to resistance to *B. tectorum* were indicators of long-term impacts: suspensions of AUMs, increases in the standard deviation of gap size among perennials, and dung from cattle since dung tends to persist in the cold desert of the Great Basin due to the absence of dung beetles and termites (Mack and Thompson 1982). Given our results, the first two factors should be thought of as indicators that the plant community has not yet recovered from past grazing disturbances (ecosystem resilience) and has not regained resistance to *B. tectorum*. Suspensions of AUMs may have been due in part to historical high levels of grazing by sheep (USDA, Forest Service 2012). The Animal Unit Equivalent of a mature sheep is 0.2, meaning that five sheep will consume the equivalent forage of one cow (Pratt and Rasmussen 2001). Sheep will browse shrubs and tend to be more selective in the grasses that they graze compared with cattle (Wilson and Harrington 1984; USDA, Forest Service 2012). Assuming that animal unit equivalents are maintained, a site being grazed by sheep is subjected to five times the number of hoofs compared with a site being grazed by cattle. Sheep also apply more total hoof pressure than cattle at the same animal units because sheep apply half the static pressure per animal 83 kPa relative to 192 kPa for cattle, but five times as many animals (Willatt and Pullar 1983). If suspended AUMs were due to sheep, the increased consumption of shrubs and increased level of trampling may explain why we observed reduced cover of shrubs with increased proportions of suspended AUMs, as sagebrush seedlings can be eliminated by trampling (Owens and Norton 1992). Although we do not have dates for when long-term grazing suspensions were implemented, we observed reduced cover of shrubs and bunchgrasses where these suspensions occurred. Even though one might expect the opposite with a reduction in grazing pressure, these indicators of grazing intensity are associated with increased cover of *B. tectorum,* but this is typical of a site that has crossed a threshold to a new stable state where nonequilibrium system processes are operating at the community level (Briske and others 2017).

Separating the current and historic effects of grazing on our study sites is nearly impossible with the use of dung counts. Dung that was present before fires likely burned on plots within fire perimeters and yet we still saw increases in dung density on burned, relative to unburned, plots, with effects associated with increased cover of *B. tectorum*. It is notable that active AUMs did not demonstrate a relationship with *B. tectorum* in our

study. Effects of the current grazing on cover of *B. tectorum* are complex as grazing can lead to reductions in cover of *B. tectorum* (Hempy-Mayer and Pyke 2009), but the timing of grazing is critical, which we were not able to account for here. However, we demonstrate a small but significant interaction between fire and grazing, as burned sites experience increased grazing pressure, leading to net negative effects on site resistance to *B. tectorum*.

This relationship between grazing history, climate, and plant responses is common across shrub grassland environments. In Australian rangelands with similar livestock grazing histories to the Great Basin (James and others 1999), plant species that responded inconsistently to grazing pressure were more likely to increase in response to grazing at higher rainfall locations and decrease at lower rainfall locations (Vesk and Westoby 2001). Grazing history of an ecosystem dictates the likelihood that the plants species present are increasers or decreasers in response to grazing. Following overgrazing of grazing-sensitive species, only increasers remain until they too are overgrazed and removed from the system (Hacker 1987; Fensham and others 1999) often leading to alternative stable states based on nonequilibrium systems. This relationship can be contrasted with rangelands in the eastern Mediterranean that have experienced domesticated grazing for approximately 5000 years and as a result, relatively fewer species are found to dramatically decrease with grazing and a greater proportion of species are found to increase likely due to selection for grazing-tolerant species (Noy-Meir and others 1989). In our system, where native perennial bunchgrasses still exist, the droughty sites may be more prone to alternative stable states and these sites may benefit from monitoring those biotic indicators more directly related to site resistance, cover of shrubs, perennial grasses, lichens, mosses, and bare soil along with distances among perennial plants. These may provide early warning indicators of resilience from fire and grazing and resistance to invasive species triggering adaptive management before alternative stable states result in undesirable invasive species. Unfortunately, we did not have data on how long a rest from grazing our sites were given following fire. Future research could examine management practices that favor the documented recovery of the biotic community following fire if maintaining site resistance to *B. tectorum* is a management goal.

We present a holistic view of fire, in the context of a history of livestock grazing for semiarid shrub grasslands, using the sagebrush steppe of the northern Great Basin as an example ecosystem. Resistance to invasive species that may result in alternative stable states appears to be linked to cover and structural composition of native perennial life-forms, including the biocrusts. Future work should examine mechanisms behind which bunchgrass and biocrust communities dictate post-disturbance site resistance and ultimately predict resilience to disturbances before these disturbances occur, thus allowing managers to prioritize their management options.

ACKNOWLEDGEMENTS

This project was funded by the US Geological Survey Coordinated Intermountain Restoration Project, US Fish and Wildlife Service, Nevada State office, US Forest Service Fire Program, and Joint Fire Science Project Number 09-S-02-1. Authors thank D. Hernandez, D. Howard, S. Lynch, and L. McCaughey for help with data collection. T. Wirth and K. Knutson helped with the use of data from the larger study. M. Germino and D. Eldridge improved the manuscript. J. Grace and B. McCune provided advice on an earlier version of the analyses and manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

REFERENCES

Andrew MH, Lange RT. 1986. Development of a new piosphere in arid chenopod shrubland grazed by sheep. II. Changes to the vegetation. Australian Journal of Ecology 11:411–24.

Aguiar MR, Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14:273–7.

Arbuckle JR. 2014. Amos (Version 23.0) [Computer Program]. Chicago: IBM SPSS.

Bowker MA, Belnap JA, Rosentreter R, Graham B. 2004. Wildfire-resistant biological soil crusts and fire-induced loss of soil stability in Palouse prairies, USA. Applied Soil Ecology 26:41–52.

Box TW. 1990. Rangelands. In: Sampson RN, Hair D, Eds. Natural resources in the 21st century. Washington DC: Island Press. p 101–20.

Boyd CS, Davies KW, Hulet A. 2015. Predicting fire-based perennial bunchgrass mortality in big sagebrush plant communities. International Journal of Wildland Fire 24(4):527–33.

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu M-N. 2017. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality and ignitions. Biological Invasions. https://dx.doi.org/10.1007/s10530-017-1641-8

Breckle SW. 1983. Temperate deserts and semi-deserts of Afghanistan and Iran. In: West NE, Ed. Ecosystems of the world

5: temperate deserts and semi-deserts. New York: Elsevier. p 271–319.

Briske DD, Illius AW, Anderies JM. 2017. Nonequilibrium ecology and resilience theory. In: Briske DD, Ed. Rangeland systems: processes, management and challenges. Cham: Springer. p 197–227.

Briske DD, Richards JH. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: Bedunah DJ, Sosebee RE, Eds. Wildland Plants: physiological ecology and development morphology. Denver, CO: Society for Range Management. p 625–710.

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keelet JB, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–88.

Bureau of Land Management. 2007. Burned area emergency stabilization and rehabilitation. U.S. Department of the Interior, Bureau of Land Management Handbook, H-1742-1, Washington DC.

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–45.

Chambers JC, Pyke DA, Maestas JD, Pellant M, Boyd CS, Campbell SB, Espinosa S, Havlina DW, Mayer KE, Wuenschel A. 2014. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. Gen. Tech. Rep. RMRS-GTR-326. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Clark PE, Lee J, Ko K, Nielson RM, Johnson DE, Ganskopp DC, Chigbrow J, Pierson FB, Hardegreee SP. 2014. Prescribed fire effects on resource selection by cattle in mesic sagebrush steppe. Part 1: spring grazing. Journal of Arid Environments 100–101:78–88.

Condon LA, Pyke DA. 2016. Gap size between perennial herbs as an index of cattle grazing impact across rangelands of the sagebrush steppe. Proceedings of the 10th International Rangeland Congress, Conference Proceedings pp 803–4.

Condon LA, Weisberg PJ. 2016. Topographic context of the burn edge influences postfire recruitment of arid land shrubs. Rangeland Ecology and Management 69:129–33.

Condon LA, Weisberg PJ, Chambers JC. 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. International Journal of Wildland Fire 20:597–604.

Cooper SV, Lesica P, Kudray GM. 2011. Post-fire recovery of Wyoming big sagebrush steppe in central and southeast Montana. Natural Resources and Environmental Issues 16:1–9.

D'Antonio CM, Chambers JC, Loh R, Tunison JT. 2009. Applying ecological concepts to the management of widespread grass invasions. In: Inderjit SK, Ed. Management of Invasive Weeds. Dordrecht: Springer Netherlands. p 123–49.

Davies KW, Bates JD, Boyd CS, Svejcar TJ. 2016. Prefire grazing by cattle increases postfire resistance to exotic annual grass (*Bromus tectorum*) invasion and dominance for decades. Ecology and Evolution 6:3356–66.

Davies KW, Bates JD, Miller RF. 2007. Environmental and vegetation relationships of *Artemisia tridentata* ssp. *wyomingensis* alliance. Journal of Arid Environments 70:478–94.

ESRI. 2013. ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.

Fenesi A, Rédei T, Botta-Dukát Z. 2011. Hard traits of three *Bromus* species in their source area explain their current invasive success. Acta Oecologica 37:441–8.

Fensham RJ, Holman JE, Cox MJ. 1999. Plant species responses along a grazing disturbance gradient in Australian grassland. Journal of Vegetation Science 10:77–86.

Fowler NL. 1988. What is a safe site? Neighbor, litter, germination date, and patch effects. Ecology 69:947–61.

Grace JB. 2006. Structural equation modeling and natural systems. New York: Cambridge University Press.

Grace JB, Schoolmaster DR Jr, Guntenspergen GR, Little AM, Mitchell BR, Miller KM, Schweiger EW. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 73:1–44.

Hacker RB. 1987. Species response to grazing and environmental factors in an arid zone halophytic shrubland community. Australian Journal of Botany 35:135–50.

Harper KT, Belnap J. 2001. The influence of biological soil crust on mineral uptake by associated vascular plants. Journal of Arid Environments 47:347–57.

Hempy-Mayer K, Pyke DA. 2009. Defoliation effects on *Bromus tectorum* seed production: implications for grazing. Rangeland Ecology and Management 61:116–23.

Herrick JE, Van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems, volume 1: Quick Start. USDA – ARS Jornada Experimental Range, Las Cruces, New Mexico.

Howery LD, Sprinkle JE, Browns JE. 2009. A summary of livestock grazing systems used on rangelands in the western United States and Canada. The University of Arizona, Cooperative Extension, AZ1184, Tucson, AZ. http://extension.arizona.edu/sites/extension.arizona.edu/files/pubs/az1184.pdf.

James CD, Landsberg J, Morton SR. 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. Journal of Arid Environments 41:87–121.

James J, Davies K, Sheley R, Aanderud Z. 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156:637–48.

Johansen JR, St. Clair LL, Webb BL, Nebeker GT. 1984. Recovery patterns of cryptogammic crusts in desert rangelands following fire disturbance. The Bryologist 87:238–43.

Kaczmarski J. 2000. Restoration implications of *Bromus tectorum*-infested grassland of the Great Basin. Restoration, Reclamation and Revegetation Research 6:1–14.

Kleiner EF, Harper KT. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecology 53:299–309.

Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, Brooks ML, Chambers JC, Grace JB. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology. https://dx.doi.org/10.1111/1365-2664.12309

Kolden CA, Smith AS, Abatzoglou JT. 2015. Limitation and utilization of Monitoring Trends in Burn Severity products for assessing wildfire severity in the USA. International Journal of Wildland Fire 24:1023–8.

Landsburg J, James CD, Morton SR, Hobbs TJ, Stol J, Drew A, Tongway H (1997) The effects of artificial sources of water on rangeland biodiversity. Biodiversity technical paper No. 3. CSIRO and Environment Australia, Canberra, Australia.

Levine JM, Adler PB, Yelenik SG. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7:975–89.

Mack RN. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agroecosystems 7:145–65.

Mack RN, Thompson JN. 1982. Evolution of steppe with few large, hooved mammals. American Naturalist 119:757–73.

McCune B, Grace JB. 2002. Analysis of Ecological Communities. Gleneden Beach, Oregon: MJM Software.

Miller RF, Chambers JC, Pyke DA, et al. 2013. A review of fire effects on vegetation and soils in the Great Basin ecoregion: response and ecological site characteristics. Gen Tech Rep RMRS-GTR-322. USDA, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Monitoring Trends in Burn Severity (MTBS). 2012. USDA Forest Service Remote Sensing Applications Center (RSAC) and the US Geological Survey National Center for Earth Resources Observation and Science (EROS). http://mtbs.gov.

Monroe AP, Aldridge CL, Assal TJ, Veblen KE, Pyke DA, Casazza ML. 2017. Patterns in Greater Sage-grouse population dynamics correspond with public grazing records at broad scales. Ecological Applications 27:1096–107.

Nelson ZJ, Weisberg PJ, Kitchen SG. 2014. Influence of climate and environment on post-fire recovery of mountain big sagebrush. International Journal of Wildland Fire 23:131–42.

Noy-Meir I, Gutman M, Kaplan Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology 77:290–310.

Owens MK, Norton BE. 1992. Interactions of grazing and plant protection on basin big sagebrush (*Artemisia tridentata* spp. *tridentata*) seedling survival. Journal of Range Management 45:257–62.

Pilliod DS, Welty JL. 2013. Land treatment digital library. U.S. Geological Survey Data Series 806. https://dx.doi.org/10.3133/ds806.

Ponzetti JM, McCune B. 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate and livestock activity. The Bryologist 104:212–25.

Ponzetti JM, McCune B, Pyke DA. 2007. Biotic soil crusts in relations to topography, cheatgrass and fire in the Columbia Basin, Washington. The Bryologist 110:706–22.

Prasse R, Bornkamm R. 2000. Effect of microbiotic soil surface crust on emergence of vascular plants. Plant Ecology 150:65–75.

Pratt M, Rasmussen A. 2001. Determining your stocking rate. Utah State University Cooperative Extension, Range Management Fact Sheet, NR/RM/04.

PRISM 2010. PRISM Climate Group, Oregon State University. http://prism.oregonstate.edu.

Pyke DA. 1987. Demographic responses of Bromus tectorum and seedlings of Agropyron spicatum to grazing by small mammals: the influence of grazing frequency and plant age. Journal of Ecology 75:825–35.

Pyke DA, Chambers JC, Pellant M, Knick ST, Miller RF, Beck JL, Doescher PS, Schupp EW, Roundy BA, Brunson M, McIver JD. 2015. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat- part 1. Concepts for understanding and applying restoration. U.S. Geological Survey Circular 1416, p 44. https://dx.doi.org/10.3133/cir1416.

Pyke DA, Chambers JC, Beck JL, Brooks ML, Mealor BA. 2016. Land uses, fire and invasion: exotic annual *Bromus* and human dimensions. In: Germino MJ, Chambers JC, Brown CS, Eds. Exotic brome-grasses in arid and semi-arid ecosystems of the Western US: causes consequences and management implications. New York: Springer. p 307–37.

Pyke DA, Shaff SE, Lindgren AI, Schupp EW, Doescher PS, Chambers JC, Burnham JS, Huso MM. 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. Rangeland Ecology and Management 67:455–67.

RAS. 2015. Rangeland Administration System, Bureau of Land Management. http://www.blm.gov/ras/, accessed 15 September 2015.

Reichenberger G, Pyke DA. 1990. Impact of early root competition on fitness components of four semiarid species. Oecologia 85:159–66.

Reisner MD, Grace JB, Pyke DA, Doescher PS. 2013. Conditions favouring Bromus tectorum dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology. https://dx.doi.org/10.1111/1365-2664.12097

Reisner MD, Doescher PS, Pyke DA. 2015. Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. Journal of Vegetation Science. https://doi.org/10.1111/jvs.12327

Rossiter NA, Setterfield SA, Douglas MM, Hutley LB. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions 9:169–76.

Ruyle G, Ogen P. 1993. What is an A.U.M.? In: Gum R, Ruyle G, Rice R, Eds. Arizona Ranchers' management guide. Arizona Cooperative Extension: Tuscon, USA. p 1–4.

Schiffman PM. 1997. Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. In: Luken JO, Thieret JW, Eds. Assessment and management of plant invasions. New York, NY: Springer-Verlag. p 87–94.

Serpe M, Orm JM, Barkes T, Rosentreter R. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecology 185:163–78.

Serpe M, Zimmerman S, Deines L, Rosentreter R. 2008. Seed water status and root tip characteristics of two annual grasses on lichen dominated biological soil crusts. Plant and Soil 303:191–205.

Stewart G, Hull AC. 1949. Cheatgrass (Bromus tectorum L.): an ecologic intruder in southern Idaho. Ecology 30:58–74.

Sugihara NG, Van Wagtendonk JW, Fites-Kaufman J. 2006. Fire as an Ecological Process. In: Sugihara NG, Van Wagtendonk JW, Shaffer KE, Fites-Kaufman J, Thode AE, Eds. Fire in California's Ecosystems. Berkeley and Los Angeles, California, USA: University of California Press. p 58–74.

Terpó A, Zajac M, Zajac A. 1999. A provisional list of Hungarian archeophytes. Thaiszia – J Bot (Kosice) 9:41–7.

U.S. Department of Agriculture, Forest Service. 2012. Future of America's Forest and Rangelands: Forest Service 2010 Resources Planning Act Assessment. Gen. Tech. Rep. WO-87. Washington, DC. p 198.

United States Department of Agriculture, Natural Resources Conservation Service (USDA NRCS). 2003. National range and pasture handbook. USDA NRCS Grazing Lands Technology Institute, Fort Worth, TX (https://www.nrcs.usda.gov/

wps/portal/nrcs/detail/national/landuse/rangepasture/?cid=stelprdb1043084 Accessed 12 July 2017).

United States Department of Agriculture, Natural Resources Conservation Service (USDA NRCS). 2006. Land resource regions and major land resource areas of the United States, the Caribbean, and the Pacific Basin. USDA Handbook 296. USDA NRCS, Washington, DC.

Veblen KE, Pyke DA, Aldridge CL, Casazza ML, Assal TJ, Farinha MA. 2014. Monitoring of livestock grazing effects on Bureau of Land Management Land. Rangeland Ecology and Management 67:68–77.

Vesk PA, Westoby M. 2001. Predicting plant species' responses to grazing. Journal of Applied Ecology 38:897–909.

Walter H, Box EO. 1983. Caspian lowland biome. In: West NE, Ed. Ecosystems of the world 5: temperate deserts and semi-deserts. New York: Elsevier. p 9–41.

West NE. 1983a. Approach. In: West NE, Ed. Ecosystems of the world 5: temperate deserts and semi-deserts. New York: Elsevier. p 1–2.

West NE. 1983b. Comparisons and contrasts between the temperate deserts and semi-deserts of three continents. In: West NE, Ed. Ecosystems of the world 5: temperate deserts and semi-deserts. New York: Elsevier. p 461–72.

West NE. 1983c. Great Basin-Colorado Plateau sagebrush semi-desert. In: West NE, Ed. Ecosystems of the world 5: temperate deserts and semi-deserts. New York: Elsevier. p 331–49.

Westerling AL, Hildalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western U.S. Forest Fire Activity. Science 313:940–3.

Willatt ST, Pullar DM. 1983. Changes in soil physical properties under grazed pastures. Australian Journal of Soil Research 22:343–8.

Wilson AD, Harrington GN. 1984. Grazing ecology and animal production. In: Harrington GN, Wilson AD, Young MD, Eds. Management of Australia's Rangelands. Melbourne, Australia: CSIRO. p 63–77.

Wright HA, Neuenschwander LF, Britton CM. 1979. The role and the uses of fire in sagebrush-grass and pinyon-juniper plant communities. A state-of-the-art review. USDA Forest Service GTR INT-58, Intermountain Forest and Range Experiment Station, Ogden, Utah. p 48.



WILEY

Guidelines to Manage Sage Grouse Populations and Their Habitats
Author(s): John W. Connelly, Michael A. Schroeder, Alan R. Sands and Clait E. Braun
Source: *Wildlife Society Bulletin (1973-2006)*, Vol. 28, No. 4 (Winter, 2000), pp. 967-985
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3783856
Accessed: 03-06-2016 14:10 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://about.jstor.org/terms

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Wildlife Society, *Wiley* are collaborating with JSTOR to digitize, preserve and extend access to *Wildlife Society Bulletin (1973-2006)*

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Guidelines to manage sage grouse populations and their habitats

John W. Connelly, Michael A. Schroeder, Alan R. Sands, and Clait E. Braun

Abstract The status of sage grouse populations and habitats has been a concern to sportsmen and biologists for >80 years. Despite management and research efforts that date to the 1930s, breeding populations of this species have declined throughout much of its range. In May 1999, the western sage grouse (*C. urophasianus phaios*) in Washington was petitioned for listing under the Endangered Species Act because of population and habitat declines (C. Warren, United States Fish and Wildlife Service, personal communication). Sage grouse populations are allied closely with sagebrush (*Artemisia* spp.). Despite the well-known importance of this habitat to sage grouse and other sagebrush obligates, the quality and quantity of sagebrush habitats have declined for at least the last 50 years. Braun et al. (1977) provided guidelines for maintenance of sage grouse habitats. Since publication of those guidelines, much more information has been obtained on sage grouse. Because of continued concern about sage grouse and their habitats and a significant amount of new information, the Western States Sage and Columbian Sharp-tailed Grouse Technical Committee, under the direction of the Western Association of Fish and Wildlife Agencies, requested a revision and expansion of the guidelines originally published by Braun et al. (1977). This paper summarizes the current knowledge of the ecology of sage grouse and, based on this information, provides guidelines to manage sage grouse populations and their habitats.

Key words *Artemisia, Centrocercus urophasianus,* guidelines, habitat, management, populations, sage grouse, sagebrush

The status of sage grouse populations and habitats has been a concern to sportsmen and biologists for >80 years (Hornaday 1916, Patterson 1952, Autenrieth 1981). Despite management and research efforts that date to the 1930s (Girard 1937), breeding populations of this species have declined by at least 17–47% throughout much of its range (Connelly and Braun 1997). In May 1999, the western sage grouse (*C. urophasianus phaios*) in Washington was petitioned for listing under the Endangered Species Act because of population and habitat declines (C. Warren, United States Fish and Wildlife Service, personal communication).

Sage grouse populations are allied closely with sagebrush (*Artemisia* spp.) habitats (Patterson 1952, Braun et al. 1977, Braun 1987). The dependence of sage grouse on sagebrush for winter habitat has been well documented (Eng and Schladweiler 1972, Beck 1975, Beck 1977, Robertson 1991). Similarly, the relationship between sagebrush

Address for John W. Connelly: Idaho Department of Fish and Game, 1345 Barton Road, Pocatello, ID 83204, USA; e-mail: JCsagegrouse@gateway.net. Address for Michael A. Schroeder: Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, WA 98813, USA. Address for Alan R. Sands: Bureau of Land Management, 1387 S. Vinnell Way, Boise, ID 83709-1657, USA; present address: The Nature Conservancy, 2404 Bank Drive, Suite 314, Boise, ID 83705, USA. Address for Clait E. Braun: Colorado Division of Wildlife, Wildlife Research Center, 317 W. Prospect Road, Fort Collins, CO 80526, USA; present address: Grouse Inc., 5572 North Ventana Vista Road, Tucson, AZ 85750-7204,USA.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms



Sage grouse on a nest with good shrub and herbaceous cover. The nest was successful.

habitats and sage grouse nest success has been described thoroughly (Klebenow 1969, Wallestad and Pyrah 1974, Wakkinen 1990, Connelly et al. 1991, Gregg et al. 1994). Despite the well-known importance of this habitat to sage grouse and other sagebrush obligates (Braun et al. 1976, Saab and Rich 1997), the quality and quantity of sagebrush habitats have declined for at least the last 50 years (Braun et al. 1976, Braun 1987, Swenson et al. 1987, Connelly and Braun 1997).

Braun et al. (1977) provided guidelines for maintenance of sage grouse habitats. Since publication of those guidelines, much more information has been obtained on relative size of sagebrush habitats used by these grouse (Connelly 1982, Connelly et al. 1988, Wakkinen et al. 1992), seasonal use of sagebrush habitats (Benson et al. 1991, Connelly et al. 1991), effects of insecticides on sage grouse (Blus et al. 1989), importance of herbaceous cover in breeding habitat (Wakkinen 1990, Connelly et al. 1991, Gregg 1991, Barnett and Crawford 1994, Drut et al. 1994*a*, Gregg et al. 1994), and effects of fire on their habitat (Hulet 1983; Benson et al. 1991; Robertson 1991; Fischer 1994; Fischer et al. 1996*a*, 1997; Pyle and Crawford 1996; Connelly et al. 2000*b*). Because of continued concern about sage grouse and their habitats and a significant amount of new information, the Western States Sage and Columbian Sharp-tailed Grouse Technical Committee, under the direction of the Western Association of Fish and Wildlife Agencies, requested a revision and expansion of the guidelines originally published by Braun et al. (1977). This paper summarizes the current knowledge of the ecology of sage grouse and, based on this information, provides guidelines to manage sage grouse populations and their habitats.

Population biology

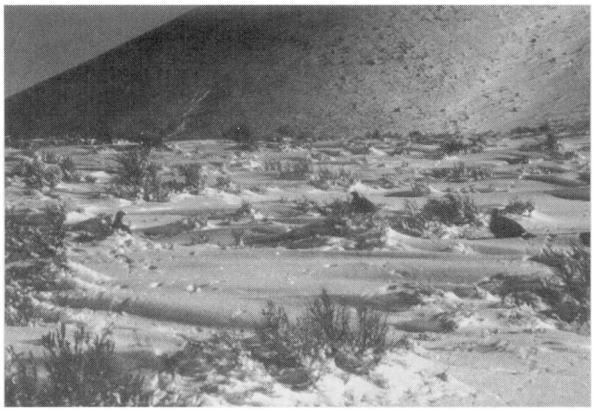
Seasonal movements and home range

Sage grouse display a variety of annual migratory patterns (Beck 1975, Wallestad 1975, Hulet 1983, Berry and Eng 1985, Connelly et al. 1988, Wakkinen 1990, Fischer 1994). Populations may have: 1) distinct winter, breeding, and summer areas; 2) distinct summer areas and integrated winter and breeding areas; 3) distinct winter areas and integrated breeding and summer areas; or 4) well-integrated seasonal habitats (nonmigratory populations). Seasonal movements between distinct seasonal ranges may exceed 75 km (Dalke et al. 1963, Connelly et al. 1988), which complicates attempts to define populations. Thus, Connelly et al. (1988) suggested that sage grouse populations be defined on a temporal and geographic basis. Because of differences in seasonal movements among populations (Dalke et al. 1963, Wallestad 1975, Connelly et al. 1988, Wakkinen 1990), 3 types of sage grouse populations can



Sage grouse on a nest with poor shrub and herbaceous cover. This nest was unsuccessful. Photo by Jena Hickey.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms



Sage grouse on winter range. Note the relatively sparse cover; without snow, the canopy cover of sagebrush in this area exceeds 20%.

be defined: 1) nonmigratory, grouse do not make long-distance movements (i.e., >10 km one way) between or among seasonal ranges; 2) one-stage migratory, grouse move between 2 distinct seasonal ranges; and 3) 2-stage migratory, grouse move among 3 distinct seasonal ranges. Within a given geographic area, especially summer range, there may be birds that belong to more than one of these types of populations.

On an annual basis, migratory sage grouse populations may occupy areas that exceed 2,700 km^2 (Hulet 1983, Leonard et al. 2000). During winter, Robertson (1991) reported that migratory sage grouse in southeastern Idaho made mean daily movements of 752 m and occupied an area ≥140 km^2. For a nonmigratory population in Montana, Wallestad (1975) reported that winter home range size ranged from 11 to 31 km^2. During summer, migratory sage grouse in Idaho occupied home ranges of 3 to 7 km^2 (Connelly and Markham 1983, Gates 1983).

Despite large annual movements, sage grouse have high fidelity to seasonal ranges (Keister and Willis 1986, Fischer et al. 1993). Females return to the same area to nest each year (Fischer et al. 1993) and may nest within 200 m of their previous year's nest (Gates 1983, Lyon 2000).

Survival

Wallestad (1975) reported that annual survival rates for yearling and adult female sage grouse were 35 and 40%, respectively, for poncho-tagged birds. However, Zablan (1993) reported that survival rates for banded yearling and adult females in Colorado were similar and averaged 55%; survival rates for yearling and adult males differed, averaging 52 and 38%, respectively. In Idaho, annual survival of male sage grouse ranged from 46 to 54% and female survival from 68 to 85% (Connelly et al. 1994). Lower survival rates for males may be related to physiological demands because of sexual dimorphism and greater predation rates (Swenson 1986).

Reproduction

Bergerud (1988) suggested that most female tetraonids nest as yearlings. Although essentially all female sage grouse nested in Washington (Schroeder 1997), Connelly et al. (1993) reported that in Idaho up to 45% of yearling and 22% of adult female sage grouse do not nest each year. Gregg (1991) indicated that, of 119 females monitored through the breeding season in eastern Oregon, 26 (22%) did not nest. However, Coggins (1998) reported a 99% nest initiation rate for 3 years for the same population in Oregon. The differences may be related to improved range condition that resulted in better nutritional status of pre-laying hens (Barnett and Crawford 1994).

Estimates of sage grouse nest success throughout the species' range vary from 12 to 86% (Trueblood 1954, Gregg 1991, Schroeder et al. 1999). Nest success also may vary on an annual basis (Schroeder 1997, Sveum et al. 1998*a*). Wallestad and Pyrah (1974) observed greater nest success by adults than yearlings. However, significant differences in nest success between age groups have not been reported in other studies (Connelly et al. 1993, Schroeder 1997).

Clutch size of sage grouse is extremely variable and relatively low compared to other species of gamebirds (Edminster 1954, Schroeder 1997). Average clutch size for first nests varies from 6.0 to



Sage grouse nest. Photo by Jena Hickey.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

9.5 throughout the species' range (Sveum 1995, Schroeder 1997). Greatest and least average clutch sizes have been reported in Washington (Sveum 1995, Schroeder 1997).

Renesting by sage grouse varies regionally from <20% (Patterson 1952, Eng 1963, Hulet 1983, Connelly et al. 1993) to >80% (Schroeder 1997). Despite regional variation, differences in renesting rates due to age have not been documented (Connelly et al. 1993, Schroeder 1997). Because of variation in nest initiation, success, and renesting rates, the proportion of females successfully hatching a brood varies between 15 and 70% (Wallestad and Pyrah 1974, Gregg et al. 1994). Despite this variation, sage grouse generally have low reproductive rates and high annual survival compared to most gallinaceous species (Zablan 1993, Connelly et al. 1994, Connelly and Braun 1997, Schroeder 1997, Schroeder et al. 1999).

Little information has been published on mortality of juvenile sage grouse or the level of production necessary to maintain a stable population. Among western states, long-term ratios have varied from 1.40 to 2.96 juveniles/hen in the fall; since 1985 these ratios have ranged from 1.21 to 2.19 (Connelly and Braun 1997). Available data suggest that a ratio ≥2.25 juveniles/hen in the fall should result in stable to increasing sage grouse populations (Connelly and Braun 1997, Edelmann et al. 1998).

Habitat requirements

Breeding habitats

Leks, or breeding display sites, typically occur in open areas surrounded by sagebrush (Patterson 1952, Gill 1965); these sites include, but are not limited to, landing strips, old lakebeds, low sagebrush flats and ridge tops, roads, cropland, and burned areas (Connelly et al. 1981, Gates 1985). Sage grouse males appear to form leks opportunistically at sites within or adjacent to potential nesting habitat. Although the lek may be an approximate center of annual ranges for nonmigratory populations (Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974), this may not be the case for migratory populations (Connelly et al. 1988, Wakkinen et al. 1992). Average distances between nests and nearest leks vary from 1.1 to 6.2 km, but distance from lek of female capture to nest may be >20 km (Autenrieth 1981, Wakkinen et al. 1992, Fischer 1994, Hanf et al. 1994, Lyon 2000). Nests are placed independent of lek location (Bradbury et al. 1989, Wakkinen et al. 1992).

Habitats used by pre-laying hens also are part of the breeding habitat. These areas should provide a diversity of forbs high in calcium, phosphorus, and protein; the condition of these areas may greatly affect nest initiation rate, clutch size, and subsequent reproductive success (Barnett and Crawford 1994, Coggins 1998).

Most sage grouse nests occur under sagebrush (Patterson 1952, Gill 1965, Gray 1967, Wallestad and Pyrah 1974), but sage grouse will nest under other plant species (Klebenow 1969, Connelly et al. 1991, Gregg 1991, Sveum et al. 1998*a*). However, grouse nesting under sagebrush experience greater nest success (53%) than those nesting under other plant species (22%, Connelly et al. 1991).

Table 1. Habitat characteristics associated with sage grouse nest sites.

	Sagebrush		Grass		
State	Height[a](cm)	Coverage (%)[b]	Height(cm)	Coverage(%)[c]	Reference
Colo.	52				Petersen 1980
Id.		15		4	Klebenow 1969
Id.	58–79	23–38			Autenrieth 1981
Id.	71	22	18	3–10	Wakkinen 1990
Id.			19–23	7–9	Connelly et al. 1991
Id.	61		22	30	Fischer 1994
Id.		15–32	15–30		Klott et al. 1993
Id.	69	19	34	15	Apa 1998
Mont.	40	27			Wallestad 1975
Oreg.	80	20			Keister and Willis 1986
Oreg.		24	14	9–32	Gregg 1991
Wash.		20		51	Schroeder 1995
Wash.		19		32	Sveum et al. 1998*a*
Wyo.	36				Patterson 1952
Wyo.	29	24	15	9	Heath et al. 1997
Wyo.	31	25	18	5	Holloran 1999
Wyo.	33	26	21	11	Lyon 2000

[a] Mean height of nest bush.
[b] Mean canopy coverage of the sagebrush surrounding the nest.
[c] Some coverage estimates may include both grasses and forbs.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Mean height of sagebrush most commonly used by nesting grouse ranges from 29 to 80 cm (Table 1), and nests tend to be under the tallest sagebrush within a stand (Keister and Willis 1986, Wakkinen 1990, Apa 1998). In general, sage grouse nests are placed under shrubs having larger canopies and more ground and lateral cover as well as in stands with more shrub canopy cover than at random sites (Wakkinen 1990, Fischer 1994, Heath et al. 1997, Sveum et al. 1998*a*, Holloran 1999). Sagebrush cover near the nest site was greater around successful nests than unsuccessful nests in Montana (Wallestad and Pyrah 1974) and Oregon (Gregg 1991). Wallestad and Pyrah (1974) also indicated that successful nests were in sagebrush stands with greater average canopy coverage (27%) than those of unsuccessful nests (20%). Gregg (1991) reported that sage grouse nest success varied by cover type. The greatest nest success occurred in a mountain big sagebrush (*A. t. tridentata vaseyana*) cover type where shrubs 40–80 cm in height had greater canopy cover at the site of successful nests than at unsuccessful nests (Gregg 1991). These observations were consistent with the results of an artificial nest study showing greater coverage of medium-height shrubs improved success of artificial nests (DeLong 1993, DeLong et al. 1995).

Grass height and cover also are important components of sage grouse nest sites (Table 1). Grass associated with nest sites and with the stand of vegetation containing the nest was taller and denser than grass at random sites (Wakkinen 1990, Gregg 1991, Sveum et al. 1998*a*). Grass height at nests under non-sagebrush plants was greater ($P<0.01$) than that associated with nests under sagebrush, further suggesting that grass height is an important habitat component for nesting sage grouse (Connelly et al. 1991). Moreover, in Oregon, grass cover was greater at successful nests than at unsuccessful nests (Gregg 1991). Grass >18 cm in height occurring in stands of sagebrush 40–80 cm tall resulted in lesser nest predation rates than in stands with lesser grass heights (Gregg et al. 1994). Herbaceous cover associated with nest sites may provide scent, visual, and physical barriers to potential predators (DeLong et al. 1995).

Early brood-rearing areas occur in upland sagebrush habitats relatively close to nest sites, but movements of individual broods may vary (Connelly 1982, Gates 1983). Within 2 days of hatching, one brood moved 3.1 km (Gates 1983). Early brood-rearing habitats may be relatively open



Radiotelemetry and a pointing dog are used to capture sage grouse chicks for a research project in southeastern Idaho.

(about 14% canopy cover) stands of sagebrush (Martin 1970, Wallestad 1971) with ≥15% canopy cover of grasses and forbs (Sveum et al. 1998*b*, Lyon 2000). Great plant species richness with abundant forbs and insects characterize brood areas (Dunn and Braun 1986, Klott and Lindzey 1990, Drut et al. 1994*a*, Apa 1998). In Oregon, diets of sage grouse chicks included 34 genera of forbs and 41 families of invertebrates (Drut et al. 1994*b*). Insects, especially ants (Hymenoptera) and beetles (Coleoptera), are an important component of early brood-rearing habitat (Drut et al. 1994*b*, Fischer et al. 1996*a*). Ants and beetles occurred more frequently ($P=0.02$) at brood-activity centers compared to nonbrood sites (Fischer et al. 1996*a*).

Summer–late brood-rearing habitats

As sagebrush habitats desiccate, grouse usually move to more mesic sites during June and July (Gill 1965, Klebenow 1969, Savage 1969, Connelly and Markham 1983, Gates 1983, Connelly et al. 1988, Fischer et al. 1996*b*). Sage grouse broods occupy a variety of habitats during summer, including sagebrush (Martin 1970), relatively small burned areas within sagebrush (Pyle and Crawford 1996), wet meadows (Savage 1969), farmland, and other irrigated areas adjacent to sagebrush habitats (Connelly and Markham 1983, Gates 1983, Connelly et al. 1988). Apa (1998) reported that sites used by grouse broods had twice as much forb cover as independent sites.

Fall habitats

Sage grouse use a variety of habitats during fall. Patterson (1952) reported that grouse move from summer to winter range in October, but during

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

mild weather in late fall, some birds may still use summer range. Similarly, Connelly and Markham (1983) observed that most sage grouse had abandoned summering areas by the first week of October. Fall movements to winter range are slow and meandering and occur from late August to December (Connelly et al. 1988). Wallestad (1975) documented a shift in feeding habits from September, when grouse were consuming a large amount of forbs, to December, when birds were feeding only on sagebrush.

Winter habitats

Characteristics of sage grouse winter habitats are relatively similar throughout most of the species' range (Table 2). Eng and Schladweiler (1972) and Wallestad (1975) indicated that most observations of radiomarked sage grouse during winter in Montana occurred in sagebrush habitats with >20% canopy cover. However, Robertson (1991) indicated that sage grouse used sagebrush habitats that had average canopy coverage of 15% and average height of 46 cm during 3 winters in southeastern Idaho. In Idaho, sage grouse selected areas with greater canopy cover of Wyoming big sagebrush (*A. t. wyomingensis*) in stands containing taller shrubs when compared to random sites (Robertson 1991).

Table 2. Characteristics of sagebrush at sage grouse winter-use sites.

State	Canopy Coverage[a] (%)	Canopy Height[a] (cm)	Reference
Colo.		24–36[bd]	Beck 1977
Colo.		20–30[cd]	Beck 1977
Colo.	43[b]	34[b]	Schoenberg 1982
Colo.	37[c]	26[c]	Schoenberg 1982
Colo.	30–38[de]	41–54[de]	Hupp 1987
Id.	38[e]	56[e]	Autenrieth 1981
Id.	26[b]	29[b]	Connelly 1982
Id.	25[c]	26[c]	Connelly 1982
Id.	15	46	Robertson 1991
Mont.	27	25	Eng and Schladweiler 1972
Mont.	>20		Wallestad 1975
Oreg.	12–17[d]		Hanf et al. 1994

[a] Mean canopy coverage or height of sagebrush above snow.
[b] Males
[c] Females
[d] Ranges are given when data were provided for more than one year or area.
[e] No snow present when measurements were made or total height of plant was measured.

In Colorado, sage grouse may be restricted to <10% of the sagebrush habitat because of variation in topography and snow depth (Beck 1977, Hupp and Braun 1989). Such restricted areas of use may not occur throughout the species' range because in southeastern Idaho, severe winter weather did not result in the grouse population greatly reducing its seasonal range (Robertson 1991).

During winter, sage grouse feed almost exclusively on leaves of sagebrush (Patterson 1952, Wallestad et al. 1975). Although big sagebrush dominates the diet in most portions of the range (Patterson 1952; Wallested et al. 1975; Remington and Braun 1985; Welch et al. 1988, 1991), low sagebrush (*A. arbuscula*), black sagebrush (*A. nova*, Dalke et al. 1963, Beck 1977), fringed sagebrush (*A. frigida*, Wallestad et al. 1975), and silver sagebrush (*A. cana*, Aldridge 1998) are consumed in many areas depending on availability. Sage grouse in some areas apparently prefer Wyoming big sagebrush (Remington and Braun 1985, Myers 1992) and in other areas mountain big sagebrush (Welch et al. 1988, 1991). Some of the differences in selection may be due to preferences for greater levels of protein and the amount of volatile oils (Remington and Braun 1985, Welch et al. 1988).

Effects of habitat alteration

Range management treatments

Breeding habitat. Until the early 1980s, herbicide treatment (primarily with 2,4-D) was the most common method to reduce sagebrush on large tracts of rangeland (Braun 1987). Klebenow (1970) reported cessation of nesting in newly sprayed areas with < 5% live sagebrush canopy cover. Nesting also was nearly nonexistent in older sprayed areas containing about 5% live sagebrush cover (Klebenow 1970). In virtually all documented cases, herbicide application to blocks of sagebrush rangeland resulted in major declines in sage grouse breeding populations (Enyeart 1956, Higby 1969, Peterson 1970, Wallestad 1975). Effects of this treatment on sage grouse populations seemed more severe if the treated area was subsequently seeded to crested wheatgrass (*Agropyron cristatum*, Enyeart 1956).

Using fire to reduce sagebrush has become more common since most uses of 2,4-D on public lands were prohibited (Braun 1987). Klebenow (1972) and Sime (1991) suggested that fire may benefit sage grouse populations. Neither Gates (1983),

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Martin (1990), nor Bensen et al. (1991) reported adverse effects of fire on breeding populations of sage grouse. In contrast, following a 9-year study, Connelly et al. (1994, 2000*b*) indicated that prescribed burning of Wyoming big sagebrush during a drought period resulted in a large decline (>80%) of a sage grouse breeding population in southeastern Idaho. Additionally, Hulet (1983) documented loss of leks from fire and Nelle et al. (2000) reported that burning mountain big sagebrush stands had long-term negative impacts on sage grouse nesting and brood-rearing habitats. Canopy cover in mountain big sagebrush did not provide appropriate nesting habitat 14 years after burning (Nelle et al. 2000). The impact of fire on sage grouse populations using habitats dominated by silver sagebrush (which may resprout following fire) is unknown.

Cheatgrass (*Bromus tectrorum*) will often occupy sites following disturbance, especially burning (Valentine 1989). Repeated burning or burning in late summer favors cheatgrass invasion and may be a major cause of the expansion of this species (Vallentine 1989). The ultimate result may be a loss of the sage grouse population because of long-term conversion of sagebrush habitat to rangeland dominated by an annual exotic grass. However, this situation largely appears confined to the western portion of the species' range and does not commonly occur in Wyoming (J. Lawson, Wyoming Department of Game and Fish, personal communication).

Mechanical methods of sagebrush control have often been applied to smaller areas than those treated by herbicides or fire, especially to convert rangeland to cropland. However, adverse effects of this type of treatment on sage grouse breeding populations also have been documented. In Montana, Swenson et al. (1987) indicated that the number of breeding males declined by 73% after 16% of their study area was plowed.

Brood-rearing habitats. Martin (1970) reported that sage grouse seldom used areas treated with herbicides to remove sagebrush in southwestern Montana. In Colorado, Rogers (1964) indicated that an entire population of sage grouse appeared to emigrate from an area that was subjected to several years of herbicide application to remove sagebrush. Similarly, Klebenow (1970) reported that herbicide spraying reduced the brood-carrying capacity of an area in southeastern Idaho. However, application of herbicides in early spring to reduce sagebrush cover may enhance some brood-rearing habitats by increasing the amount of herbaceous plants used for food (Autenrieth 1981).

Fire may improve sage grouse brood-rearing habitat (Klebenow 1972, Gates 1983, Sime 1991), but until recently, experimental evidence was not available to support or refute these contentions (Braun 1987). Pyle and Crawford (1996) suggested that fire may enhance brood-rearing habitat in montane settings but cautioned that its usefulness requires further investigation. A 9-year study of the effects of fire on sage grouse did not support that prescribed fire, conducted during late summer in a Wyoming big sagebrush habitat, improved brood-rearing habitat for sage grouse (Connelly et al. 1994, Fischer et al. 1996*a*). Prescribed burning of sage grouse habitat did not increase amount of forbs in burned areas compared to unburned areas (Fischer et al. 1996*a*, Nelle et al. 2000) and resulted in decreased insect populations in the treated area compared to the unburned area. Thus, fire may negatively affect sage grouse brood-rearing habitat rather than improve it in Wyoming big sagebrush habitats (Connelly and Braun 1997), but its effect on grouse habitats in mountain big sagebrush communities requires further investigation (Pyle and Crawford 1996, Nelle et al. 2000).

Sage grouse often use agricultural areas for brood-rearing habitat (Patterson 1952, Wallestad 1975, Gates 1983, Connelly et al. 1988, Blus et al. 1989). Grouse use of these areas may result in mortality because of exposure to insecticides. Blus et al. (1989) reported die-offs of sage grouse that were exposed to methamidiphos used in potato fields and dimethoate used in alfalfa fields. Dimethoate is used commonly for alfalfa, and 20 of 31 radiomarked grouse (65%) died following direct exposure to this insecticide (Blus et al. 1989).

Winter habitat. Reduction in sage grouse use of an area treated by herbicide was proportional to the severity (i.e., amount of damage to sagebrush) of the treatment (Pyrah 1972). In sage grouse winter range, strip partial kill, block partial kill, and total kill of sagebrush were increasingly detrimental to sage grouse in Montana (Pyrah 1972) and Wyoming (Higby 1969).

In Idaho, Robertson (1991) reported that a 2,000-ha prescribed burn that removed 57% of the sagebrush cover in sage grouse winter habitat minimally impacted the sage grouse population. Although sage grouse use of the burned area declined following the fire, grouse adapted to this disturbance by moving 1 to 10 km outside of the burn to areas

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

with greater sagebrush cover (Robertson 1991) than was available in the burned area.

Land use

Mining-energy development. Effects of mining, oil, and gas developments on sage grouse populations are not well known (Braun 1998). These activities negatively impact grouse habitat and populations over the short term (Braun 1998), but research suggests some recovery of populations following initial development and subsequent reclamation of the affected sites (Eng et al. 1979, Tate et al. 1979, Braun 1986). In Colorado, sage grouse were displaced by oil development and coal-mining activities, but numbers returned to pre-disturbance levels once the activities ceased (Braun 1987, Remington and Braun 1991). At least 6 leks in Alberta were disturbed by energy development and 4 were abandoned (Aldridge 1998). In Wyoming, female sage grouse captured on leks disturbed by natural gas development had lower nest-initiation rates, longer movements to nest sites, and different nesting habitats than hens captured on undisturbed leks (Lyon 2000). Sage grouse may repopulate an area following energy development but may not attain population levels that occurred prior to development (Braun 1998). Thus, short-term and long-term habitat loss appears to result from energy development and mining (Braun 1998).

Grazing. Domestic livestock have grazed over most areas used by sage grouse and this use is generally repetitive with annual or biennial grazing periods of varying timing and length (Braun 1998). Grazing patterns and use of habitats are often dependent on weather conditions (Valentine 1990). Historic and scientific evidence indicates that livestock grazing did not increase the distribution of sagebrush (Peterson 1995) but markedly reduced the herbaceous understory over relatively large areas and increased sagebrush density in some areas (Vale 1975, Tisdale and Hironaka 1981). Within the intermountain region, some vegetation changes from livestock grazing likely occurred because sagebrush steppe in this area did not evolve with intensive grazing by wild herbivores, as did the grassland prairies of central North America (Mack and Thompson 1982). Grazing by wild ungulates may reduce sagebrush cover (McArthur et al. 1988, Peterson 1995), and livestock grazing may result in high trampling mortality of sagebrush seedlings (Owens and Norton 1992). In Wyoming big sagebrush habitats, resting areas from livestock grazing may improve understory production as well as decrease sagebrush cover (Wambolt and Payne 1986).

There is little direct experimental evidence linking grazing practices to sage grouse population levels (Braun 1987, Connelly and Braun 1997). However, grass height and cover affect sage grouse nest site selection and success (Wakkinen 1990, Gregg 1991, Gregg et al. 1994, Delong et al. 1995, Sveum et al. 1998*a*). Thus, indirect evidence suggests grazing by livestock or wild herbivores that significantly reduces the herbaceous understory in breeding habitat may have negative impacts on sage grouse populations (Braun 1987, Dobkin 1995).

Miscellaneous activities. Construction of roads, powerlines, fences, reservoirs, ranches, farms, and housing developments has resulted in sage grouse habitat loss and fragmentation (Braun 1998). Between 1962 and 1997, >51,000 km of fence were constructed on land administered by the Bureau of Land Management in states supporting sage grouse populations (T. D. Rich, United States Bureau of Land Management, personal communication). Structures such as powerlines and fences pose hazards to sage grouse because they provide additional perch sites for raptors and because sage grouse may be injured or killed when they fly into these structures (Call and Maser 1985).

Weather

Prolonged drought during the 1930s and mid-1980s to early 1990s coincided with declining sage grouse populations throughout much of the species' range (Patterson 1952, Fischer 1994, Hanf et al. 1994). Drought may affect sage grouse populations by reducing herbaceous cover at nests and the quantity and quality of food available for hens and chicks during spring (Hanf et al. 1994, Fischer et al. 1996*a*).

Spring weather may influence sage grouse production. Relatively wet springs may result in increased production (Wallestad 1975, Autenrieth 1981). However, heavy rainfall during egg-laying or unseasonably cold temperatures with precipitation during hatching may decrease production (Wallestad 1975).

There is no evidence that severe winter weather affects sage grouse populations unless sagebrush cover has been greatly reduced or eliminated (Wallestad 1975, Beck 1977, Robertson 1991).

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Predation

Over the last 25 years, numerous studies have used radiotelemetry to address sage grouse survival and nest success (Wallestad 1975; Hulet 1983; Gregg 1991; Robertson 1991; Connelly et al. 1993, 1994; Gregg et al. 1994; Schroeder 1997). Only Gregg (1991) and Gregg et al. (1994) indicated that predation was limiting sage grouse numbers, and their research suggested that low nest success from predation was related to poor nesting habitat. Most reported nest-success rates are >40%, suggesting that nest predation is not a widespread problem. Similarly, high survival rates of adult (Connelly et al. 1993, Zablan 1993) and older (>10 weeks of age) juvenile sage grouse indicate that population declines are not generally related to high levels of predation. Thus, except for an early study in Oregon (Batterson and Morse 1948), predation has not been identified as a major limiting factor for sage grouse (Connelly and Braun 1997).

Constructing ranches, farms, and housing developments has resulted in the addition of nonnative predators to sage grouse habitats, including dogs, cats, and red foxes (*Vulpes vulpes*; J. W. Connelly, Idaho Department of Fish and Game, unpublished data; B. L. Welch, United States Forest Service, personal communication) and may be responsible for increases in abundance of the common raven (*Corvus corax*, Sauer et al. 1997). Relatively high raven populations may decrease sage grouse nest success (Batterson and Morse 1948, Autenrieth 1981), but rigorous field studies using radiotelemetry do not support this hypothesis. Current work in Strawberry Valley, Utah, suggests that red foxes are taking a relatively high proportion of the population (Flinders 1999). This may become a greater problem if red foxes become well established throughout sage grouse breeding habitat.

Recommended guidelines

Sage grouse populations occupy relatively large areas on a year-round basis (Berry and Eng 1985, Connelly et al. 1988, Wakkinen 1990, Leonard et al. 2000), invariably involving a mix of ownership and jurisdictions. Thus, state and federal natural resource agencies and private landowners must coordinate efforts over at least an entire seasonal range to successfully implement these guidelines. Based on current knowledge of sage grouse population and habitat trends, these guidelines have been developed to help agencies and landowners effectively assess and manage populations, protect and manage remaining habitats, and restore damaged habitat. Because of gaps in our knowledge and regional variation in habitat characteristics (Tisdale and Hironaka 1981), the judgment of local biologists and quantitative data from population and habitat monitoring are necessary to implement the guidelines correctly. Further, we urge agencies to use an adaptive management approach (Macnab 1983, Gratson et al. 1993), using monitoring and evaluation to assess the success of implementing these guidelines to manage sage grouse populations.

Activities responsible for the loss or degradation of sagebrush habitats also may be used to restore these habitats. These activities include prescribed fire, grazing, herbicides, and mechanical treatments. Decisions on land treatments using these tools should be based on quantitative knowledge of vegetative conditions over an entire population's seasonal range. Generally, the treatment selected should be that which is least disruptive to the vegetation community and has the most rapid recovery time. This selection should not be based solely on economic cost.

Definitions

For the purpose of these guidelines, we define an occupied lek as a traditional display area in or adjacent to sagebrush-dominated habitats that has been attended by ≥2 male sage grouse in ≥2 of the previous 5 years. We define a breeding population as a group of birds associated with 1 or more occupied leks in the same geographic area separated from other leks by >20 km. This definition is somewhat arbitrary but generally based on maximum distances females move to nest.

Population management

1) Before making management decisions, agencies should cooperate to first identify lek locations and determine whether a population is migratory or nonmigratory. In the case of migratory populations, migration routes and seasonal habitats must be identified to allow for meaningful and correct management decisions.

2) Breeding populations should be assessed by either lek counts (census number of males attending leks) or lek surveys (classify known leks as active or inactive) each year (Autenrieth et al. 1982). Depending on number of counts each spring (Jenni and Hartzler 1978, Emmons and Braun

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

1984) and weather conditions when the counts were made, lek counts may not provide an accurate assessment of sage grouse populations (Beck and Braun 1980) and the data should be viewed with caution. Despite these shortcomings, lek counts provide the best index to breeding population levels and many long-term data sets are available for trend analysis (Connelly and Braun 1997).

3) Production or recruitment should be monitored by brood counts or wing surveys (Autenrieth et al. 1982). Brood counts are labor-intensive and usually result in inadequate sample size. Where adequate samples of wings can be obtained, we recommend using wing surveys to obtain estimates of sage grouse nesting success and juvenile:adult hen (including yearlings) ratios.

4) Routine population monitoring should be used to assess trends and identify problems for all hunted and nonhunted populations. Check stations, wing collections, and questionnaires can be used to obtain harvest information. Breeding population and production data (above) can be used to monitor nonhunted populations.

5) The genetic variation of relatively small, isolated populations should be documented to better understand threats to these populations and implement appropriate management actions (Young 1994, Oyler-McCance et al. 1999).

6) Hunting seasons for sage grouse should be based on careful assessments of population size and trends. Harvest should not be based on the observations of Allen (1954:43), who stated, "Our populations of small animals operate under a 1-year plan of decimation and replacement; and Nature habitually maintains a wide margin of overproduction. She kills off a huge surplus of animals whether we take our harvest or not." To the contrary, sage grouse tend to have relatively long lives with low annual turnover (Zablan 1993, Connelly et al. 1994) and a low reproductive rate (Gregg 1991, Connelly et al. 1993). Consequently, hunting may be additive to other causes of mortality for sage grouse (Johnson and Braun 1999, Connelly et al. 2000*a*). However, most populations appear able to sustain hunting if managed carefully (Connelly et al. 2000*a*).

7) If populations occur over relatively large geographic areas and are stable to increasing, seasons and bag limits can be relatively liberal (2- to 4-bird daily bag limit and a 2- to 5-week season) for hunting seasons allowing firearms (Braun and Beck 1985).

8) If populations are declining (for 3 or more consecutive years) or trends are unknown, seasons and bag limits should be generally conservative (1- or 2-bird daily bag limit and a 1-to 4-week season) for hunting seasons allowing firearms, or suspended (for all types of hunting, including falconry and Native American subsistence hunting) because of this species' population characteristics (Braun 1998, Connelly et al. 2000*a*).

9) Where populations are hunted, harvest rates should be 10% or less of the estimated fall population to minimize negative effects on the subsequent year's breeding population (Connelly et al. 2000*a*).

10) Populations should not be hunted where ≤300 birds comprise the breeding population (i.e., ≤100 males are counted on leks [C. E. Braun, Colorado Division of Wildlife, unpublished report]).

11) Spring hunting of sage grouse on leks should be discouraged or, if unavoidable, confined to males only during the early portion of the breeding season. Spring hunting is considered an important tradition for some Native American tribes. However, in Idaho, 80% of the leks hunted during spring in the early 1990s (n=5) had become inactive by 1994 (Connelly et al. 1994).

12) Viewing sage grouse on leks (and censusing leks) should be conducted so that disturbance to birds is minimized or preferably eliminated (Call and Maser 1986). Agencies should generally not provide all lek locations to individuals simply interested in viewing birds. Instead, 1 to 3 lek locations should be identified as public viewing leks, and if demand is great enough, agencies should consider erecting 2–3 seasonal blinds at these leks for public use. Camping in the center of or on active leks should be vigorously discouraged.

13) Discourage establishment of red fox and other nonnative predator populations in sage grouse habitats.

14) For small, isolated populations and declining populations, assess the impact of predation on survival and production. Predator control programs are expensive and often ineffective. In some cases, these programs may provide temporary help while habitat is recovering. Predator management programs also could be considered in areas where seasonal habitats are in good condition but their extent has been reduced greatly. However, predator management should be implemented only if the available data (e.g., nest success <25%, annual survival of adult hens <45%) support the action.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

General habitat management

The following guidelines pertain to all seasonal habitats used by sage grouse:

1) Monitor habitat conditions and propose treatments only if warranted by range condition (i.e., the area no longer supports habitat conditions described in the following guidelines under habitat protection). Do not base land treatments on schedules, targets, or quotas.

2) Use appropriate vegetation treatment techniques (e.g., mechanical methods, fire) to remove junipers and other conifers that have invaded sage grouse habitat (Commons et al. 1999). Whenever possible, use vegetation control techniques that are least disruptive to the stand of sagebrush, if this stand meets the needs of sage grouse (Table 3).

Table 3. Characteristics of sagebrush rangeland needed for productive sage grouse habitat.

	Breeding		Brood-rearing		Winter[e]	
	Height (cm)	Canopy (%)	Height (cm)	Canopy (%)	Height (cm)	Canopy (%)
Mesic sites[a]						
Sagebrush	40–80	15–25	40–80	10–25	25–35	10–30
Grass–forb	>18[c]	≥25[d]	variable	>15	N/A	N/A
Arid sites[a]						
Sagebrush	30–80	15–25	40–80	10–25	25–35	10–30
Grass/forb	>18[c]	≥15	variable	>15	N/A	N/A
Area[b]	>80		>40		>80	

[a] Mesic and arid sites should be defined on a local basis; annual precipitation, herbaceous understory, and soils should be considered (Tisdale and Hironaka 1981, Hironaka et al. 1983).

[b] Percentage of seasonal habitat needed with indicated conditions.

[c] Measured as "droop height"; the highest naturally growing portion of the plant.

[d] Coverage should exceed 15% for perennial grasses and 10% for forbs; values should be substantially greater if most sagebrush has a growth form that provides little lateral cover (Schroeder 1995)

[e] Values for height and canopy coverage are for shrubs exposed above snow.1

3) Increase the visibility of fences and other structures occurring within 1 km of seasonal ranges by flagging or similar means if these structures appear hazardous to flying grouse (e.g., birds have been observed hitting or narrowly missing these structures or grouse remains have been found next to these structures).

4) Avoid building powerlines and other tall structures that provide perch sites for raptors within 3 km of seasonal habitats. If these structures must be built, or presently exist, the lines should be buried or poles modified to prevent their use as raptor perch sites.

Breeding habitat management

For migratory and nonmigratory populations, lek attendance, nesting, and early brood rearing occur in breeding habitats. These habitats are sagebrush-dominated rangelands with a healthy herbaceous understory and are critical for survival of sage grouse populations. Mechanical disturbance, prescribed fire, and herbicides can be used to restore sage grouse habitats to those conditions identified as appropriate in the following sections on habitat protection. Local biologists and range ecologists should select the appropriate technique on a case-by-case basis. Generally, fire should not be used in breeding habitats dominated by Wyoming big sagebrush if these areas support sage grouse. Fire can be difficult to control and tends to burn the best remaining nesting and early brood-rearing habitats (i.e., those areas with the best remaining understory), while leaving areas with poor understory. Further, we recommend against using fire in habitats dominated by xeric mountain big sagebrush (*A. t. xericensis*) because annual grasses commonly invade these habitats and much of the original habitat has been altered by fire (Bunting et al. 1987).

Although mining and energy development are common activities throughout the range of sage grouse, quantitative data on the long-term effects of these activities on sage grouse are limited. However, some negative impacts have been documented (Braun 1998, Lyon 2000). Thus, these activities should be discouraged in breeding habitats, but when they are unavoidable, restoration efforts should follow procedures outlined in these guidelines.

Habitat protection

1) Manage breeding habitats to support 15–25% canopy cover of sagebrush, perennial herbaceous cover averaging ≥18 cm in height with ≥15% canopy cover for grasses and ≥10% for forbs and a diversity of forbs (Barnett and Crawford 1994, Drut et al. 1994*a*, Apa 1998) during spring (Table 3). Habitats meeting these conditions should have a high priority for wildfire suppression and should

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

not be considered for sagebrush control programs. Sagebrush and herbaceous cover should provide overhead and lateral concealment from predators. If average sagebrush height is >75 cm, herbaceous cover may need to be substantially greater than 18 cm to provide this protection. There is much variability among sagebrush-dominated habitats (Tisdale and Hironaka 1981, Hironaka et al. 1983), and some Wyoming sagebrush and low sagebrush breeding habitats may not support 25% herbaceous cover. In these areas, total herbaceous cover should be ≥15 % (Table 3). Further, the herbaceous height requirement may not be possible in habitats dominated by grasses that are relatively short when mature. In all of these cases, local biologists and range ecologists should develop height and cover requirements that are reasonable and ecologically defensible. Leks tend to be relatively open, thus cover on leks should not meet these requirements.

2) For nonmigratory grouse occupying habitats that are distributed uniformly (i.e., habitats have the characteristics described in guideline 1 and are generally distributed around the leks), protect (i.e., do not manipulate) sagebrush and herbaceous understory within 3.2 km of all occupied leks. For nonmigratory populations, consider leks the center of year-round activity and use them as focal points for management efforts (Braun et al. 1977).

3) For nonmigratory populations where sagebrush is not distributed uniformly (i.e., habitats have the characteristics described in guideline 1 but distributed irregularly with respect to leks), protect suitable habitats for ≤5 km from all occupied leks. Use radiotelemetry, repeated surveys for grouse use, or habitat mapping to identify nesting and early brood-rearing habitats.

4) For migratory populations, identify and protect breeding habitats within 18 km of leks in a manner similar to that described for nonmigratory sage grouse. For migratory sage grouse, leks generally are associated with nesting habitats but migratory birds may move >18 km from leks to nest sites. Thus, protection of habitat within 3.2 km of leks may not protect most of the important nesting areas (Wakkinen et al. 1992, Lyon 2000).

5) In areas of large-scale habitat loss (≥40% of original breeding habitat), protect all remaining habitats from additional loss or degradation. If remaining habitats are degraded, follow guidelines for habitat restoration listed below.

6) During drought periods (≥2 consecutive years), reduce stocking rates or change management practices for livestock, wild horses, and wild ungulates if cover requirements during the nesting and brood-rearing periods are not met. Grazing pressure from domestic livestock and wild ungulates should be managed in a manner that at all times addresses the possibility of drought.



Sage grouse just leaving a nest in good-condition breeding habitat in southwestern Idaho. Note the height of grass and herbaceous cover.

7) Suppress wildfires in all breeding habitats. In the event of multiple fires, land management agencies should have all breeding habitats identified and prioritized for suppression, giving the greatest priority to those that have become fragmented or reduced by >40% in the last 30 years.

8) Adjust timing of energy exploration, development, and construction activity to minimize disturbance of sage grouse breeding activities. Energy-related facilities should be located >3.2 km from active leks whenever possible. Human activities within view of or <0.5 km from leks should be minimized during the early morning and late evening when birds are near or on leks.

Habitat restoration

1) Before initiating vegetation treatments, quantitatively evaluate the area proposed for treatment to ensure that it does not have sagebrush and herbaceous cover suitable for breeding habitat (Table 3). Treatments should not be undertaken within sage grouse habitats until the limiting vegetation factor(s) has been identified, the proposed treatment is known to provide the desired vegetation response, and land-use activities can be managed after treatment to ensure that vegetation objectives are met.

2) Restore degraded rangelands to a condition that again provides suitable breeding habitat for sage grouse by including sagebrush, native forbs

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

(especially legumes), and native grasses in reseeding efforts (Apa 1998). If native forbs and grasses are unavailable, use species that are functional equivalents and provide habitat characteristics similar to those of native species.

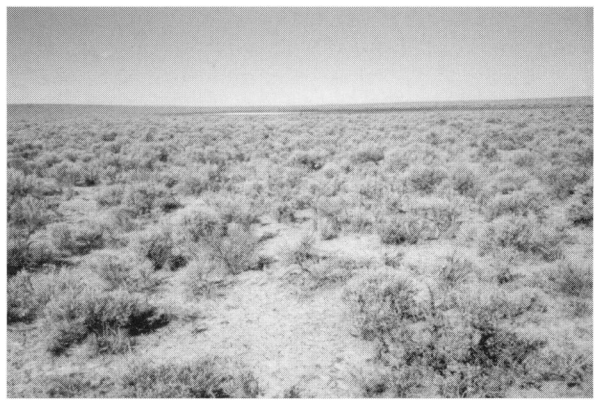
3) Where the sagebrush overstory is intact but the understory has been degraded severely and quality of nesting habitat has declined (Table 3), use appropriate techniques (e.g., brush beating in strips or patches and interseed with native grasses and forbs) that retain some sagebrush but open shrub canopy to encourage forb and grass growth.

4) Do not use fire in sage grouse habitats prone to invasion by cheatgrass and other invasive weed species unless adequate measures are included in restoration plans to replace the cheatgrass understory with perennial species using approved reseeding strategies. These strategies could include, but are not limited to, use of pre-emergent herbicides (e.g., Oust®, Plateau®) to retard cheatgrass germination until perennial herbaceous species become established.

5) When restoring habitats dominated by Wyoming big sagebrush, regardless of the techniques used (e.g., prescribed fire, herbicides), do not treat >20% of the breeding habitat (including areas burned by wildfire) within a 30-year period (Bunting et al. 1987). The 30-year period represents the approximate recovery time for a stand of Wyoming big sagebrush. Additional treatments should be deferred until the previously treated area again provides suitable breeding habitat (Table 3). In some cases, this may take <30 years and in other cases >30 years. If 2,4-D or similar herbicides are used, they should be applied in strips such that their effect on forbs is minimized. Because fire generally burns the best remaining sage grouse habitats (i.e., those with the best understory) and leaves areas with sparse understory, use fire for habitat restoration only when it can be convincingly demonstrated to be in the best interest of sage grouse.



Nest habitat is measured in Owyhee County, southwestern Idaho.



This breeding habitat is in poor condition because of a lack of understory.

6) When restoring habitats dominated by mountain big sagebrush, regardless of the techniques used (e.g., fire, herbicides), treat ≤20% of the breeding habitat (including areas burned by wildfire) within a 20-year period (Bunting et al. 1987). The 20-year period represents the approximate recovery time for a stand of mountain big sagebrush. Additional treatments should be deferred until the previously treated area again provides suitable breeding habitat (Table 3). In some cases, this may take <20 years and in other cases >20 years. If 2,4-D or similar herbicides are used, they should be applied in strips such that their effect on forbs is minimized.

7) All wildfires and prescribed burns should be evaluated as soon as possible to determine whether reseeding is necessary to achieve habitat management objectives. If needed, reseed with sagebrush, native bunchgrasses, and forbs whenever possible.

8) Until research unequivocally demonstrates that using tebuthiuron and similar-acting herbicides to control sagebrush has no long-lasting negative impacts on sage grouse habitat, use these herbicides only on an experimental basis and over a sufficiently small area that any long-term negative impacts are negligible. Because these herbicides have the potential of reducing but not eliminating sagebrush cover within grouse breeding habitats, thus stimulating herbaceous development, their use as sage grouse habitat management tools should be examined closely.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms



John Crawford explains Oregon's sage grouse research program to field-trip attendees during a meeting of the Western States Sage and Columbian sharp-tailed Grouse Technical Committee.

Summer–late brood-rearing habitat management

Sage grouse may use a variety of habitats, including meadows, farmland, dry lakebeds, sagebrush, and riparian zones from late June to early November (Patterson 1952, Wallestad 1975, Connelly 1982, Hanf et al. 1994). Generally, these habitats are characterized by relatively moist conditions and many succulent forbs in or adjacent to sagebrush cover.

Habitat protection

1) Avoid land-use practices that reduce soil moisture effectiveness, increase erosion, cause invasion of exotic plants, and reduce abundance and diversity of forbs.

2) Avoid removing sagebrush within 300 m of sage grouse foraging areas along riparian zones, meadows, lakebeds, and farmland, unless such removal is necessary to achieve habitat management objectives (e.g., meadow restoration, treatment of conifer encroachment).

3) Discourage use of very toxic organophosphorus and carbamate insecticides in sage grouse brood-rearing habitats. Sage grouse using agricultural areas may be adversely affected by pesticide applications (Blus et al. 1989). Less toxic agrichemicals or biological control may provide suitable alternatives in these areas.

4) Avoid developing springs for livestock water, but if water from a spring will be used in a pipeline or trough, design the project to maintain free water and wet meadows at the spring. Capturing water from springs using pipelines and troughs may adversely affect wet meadows used by grouse for foraging.

Habitat restoration

1) Use brush beating or other mechanical treatments in strips 4–8 m wide in areas with relatively high shrub-canopy cover (≥35% total shrub cover) to improve late brood-rearing habitats. Brush beating can be used to effectively create different age classes of sagebrush in large areas with little age diversity.

2) If brush beating is impractical, use fire or herbicides to create a mosaic of openings in mountain big sagebrush and mixed-shrub communities used as late brood-rearing habitats where total shrub cover is ≥35%. Generally, 10–20% canopy cover of sagebrush and ≤25% total shrub cover will provide adequate habitat for sage grouse during summer.

3) Construct water developments for sage grouse only in or adjacent to known summer-use areas and provide escape ramps suitable for all avian species and other small animals. Water developments and "guzzlers" may improve sage grouse summer habitats (Autenrieth et al. 1982, Hanf et al. 1994). However, sage grouse used these developments infrequently in southeastern Idaho because most were constructed in sage grouse winter and breeding habitat rather than summer range (Connelly and Doughty 1989).

4) Whenever possible, modify developed springs and other water sources to restore natural free-flowing water and wet meadow habitats.

Winter habitat management

Sagebrush is the essential component of winter habitat. Sage grouse select winter-use sites based on snow depth and topography, and snowfall can affect the amount and height of sagebrush available to grouse (Connelly 1982, Hupp and Braun 1989, Robertson 1991). Thus, on a landscape scale, sage grouse winter habitats should allow grouse access to sagebrush under all snow conditions (Table 3).

Habitat protection

1) Maintain sagebrush communities on a landscape scale, allowing sage grouse access to sagebrush stands with canopy cover of 10–30% and heights of at least 25–35 cm regardless of snow cover. These areas should be high priority for wildfire suppression and sagebrush control should be avoided.

2) Protect patches of sagebrush within burned areas from disturbance and manipulation. These areas may provide the only winter habitat for sage grouse and their loss could result in the extirpation of the grouse population. They also are important

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

seed sources for sagebrush re-establishment in the burned areas. During fire-suppression activities do not remove or burn any remaining patches of sagebrush within the fire perimeter.

3) In areas of large-scale habitat loss (≥40% of original winter habitat), protect all remaining sagebrush habitats.

Habitat restoration

1) Reseed former winter range with the appropriate subspecies of sagebrush and herbaceous species unless the species are recolonizing the area in a density that would allow recovery (Table 3) within 15 years.

2) Discourage prescribed burns >50 ha, and do not burn >20% of an area used by sage grouse during winter within any 20–30-year interval (depending on estimated recovery time for the sagebrush habitat).

Conservation strategies

We recommend that each state and province develop and implement conservation plans for sage grouse. These plans should use local working groups comprised of representatives of all interested agencies, organizations, and individuals to identify and solve regional issues (Anonymous 1997). Within the context of these plans, natural resource agencies should cooperate to document the amount and condition of sagebrush rangeland remaining in the state or province. Local and regional plans should summarize common problems to conserve sage grouse and general conditions (Table 3) needed to maintain healthy sage grouse populations. Local differences in conditions that affect sage grouse populations may occur and should be considered in conservation plans. Natural resource agencies should identify remaining breeding and winter ranges in Wyoming big sagebrush habitats and establish these areas as high priority for wildfire suppression. Prescribed burning in habitats that are in good ecological condition should be avoided. Protection and restoration of sage grouse habitats also will likely benefit many other sagebrush obligate species (Saab and Rich 1997) and enhance efforts to conserve and restore sagebrush steppe.

Although translocating sage grouse to historical range has been done on numerous occasions, few attempts have been successful (Musil et al. 1993, Reese and Connelly 1997). Thus, we agree with Reese and Connelly (1997) that translocation efforts should be viewed as only experimental at this time and not as a viable management strategy.

More information is needed on characteristics of healthy sagebrush ecosystems and the relationship of grazing to sage grouse production. Field experiments should be implemented to evaluate the relationship of grazing pressure (i.e., disturbance and removal of herbaceous cover) to sage grouse nest success and juvenile survival (Connelly and Braun 1997). The overall quality of existing sage grouse habitat will become increasingly important as quantity of these habitats decrease. Sage grouse populations appear relatively secure in some portions of their range and at risk in other portions. However, populations that have thus far survived extensive habitat loss may still face extinction because of a time lag between habitat loss and ultimate population collapse (Cowlishaw 1999).

Acknowledgments. This is a contribution from Colorado Federal Aid in Wildlife Restoration Project W-167-R, Idaho Federal Aid in Wildlife Restoration Project W-160-R, and Washington Federal Aid in Wildlife Restoration Project W-96-R. We thank state and federal representatives to the Western States Sage and Columbian Sharp-tailed Grouse Technical Committee for providing comments on earlier drafts. We are very grateful to A. D. Apa, J. A. Crawford, J. T. Flinders, T. P. Hemker, M. Pellant, and T. D. Rich for their contributions to the development of these guidelines. We also thank K. P. Reese and an anonymous reviewer for helpful comments on this manuscript. Finally, we greatly appreciate the thoughts and suggestions provided by many other individuals interested in conservation and management of sage grouse.

Literature cited

ALDRIDGE, C. L. 1998. Status of the sage grouse (*Centrocercus urophasianus urophasianus*) in Alberta. Alberta Environmental Protection, Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report 13, Edmonton, Canada.

ALLEN, D. L. 1954. Our wildlife legacy. Funk and Wagnalls, New York, New York, USA.

ANONYMOUS. 1997. Gunnison sage grouse conservation plan, Gunnison Basin, Colorado. Colorado Division of Wildlife, Fort Collins, USA.

APA, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. Dissertation, University of Idaho, Moscow, USA.

AUTENRIETH, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Wildlife Bulletin 9, Boise, Idaho, USA.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

AUTENRIETH, R. E., W. MOLINI, AND C. E. BRAUN. 1982. Sage grouse management practices. Western States Sage Grouse Committee, Technical Bulletin 1, Twin Falls, Idaho, USA.

BARNETT, J. F., AND J. A. CRAWFORD. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47: 114-118.

BATTERSON, W. M., AND W. B. MORSE. 1948. Oregon sage grouse. Oregon Game Commission Fauna Series 1, Portland, USA.

BECK, T. D. I. 1975. Attributes of a wintering population of sage grouse, North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

BECK, T. D. I. 1977. Sage grouse flock characteristics and habitat selection during winter. Journal of Wildlife Management 41: 18-26.

BECK, T. D. I., AND C. E. BRAUN. 1980. The strutting ground count: variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies 60: 558-566.

BENSON, L. A., C. E. BRAUN, AND W. C. LEININGER. 1991. Sage grouse response to burning in the big sagebrush type. Proceedings, issues and technology in the management of impacted western wildlife. Thorne Ecological Institute 5: 97-104.

BERGERUD, A. T. 1988. Population ecology of North American grouse. Pages 578-648 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota, Minneapolis, USA.

BERRY, J. D., AND R. L. ENG. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. Journal of Wildlife Management 49: 237-240.

Blus, L. J., C. S. Staley, C. J. Henny, G. W. Pendleton, T. H. Craig, E. H. Craig, and D. K. HALFORD. 1989. Effects of organophosphorus insecticides on sage grouse in southeastern Idaho. Journal of Wildlife Management 53: 1139-1146.

BRADBURY, J. W., R. M. GIBSON, C. E. MCCARTHY, AND S. L. VEHRENCAMP. 1989. Dispersion of displaying male sage grouse. II. The role of female dispersion. Behavioral Ecology and Sociobiology 24: 15-24.

BRAUN, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. Proceedings, issues and technology in the management of impacted western wildlife. Thorne Ecological Institute 2: 227-231.

BRAUN, C. E. 1987. Current issues in sage grouse management. Proceedings of the Western Association of Fish and Wildlife Agencies 67: 134-144.

BRAUN, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78: 139-156.

BRAUN, C. E., AND T. D. I BECK. 1985. Effects of changes in hunting regulations on sage grouse harvest and populations. Pages 335-344 *in* S. L. Beasom and S. F. Roberson, editors. Game harvest management. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.

BRAUN C. E., T. BRITT, AND R. O. WALLESTAD. 1977. Guidelines for maintenance of sage grouse habitats. Wildlife Society Bulletin 5: 99-106.

BRAUN C. E., M. F. BAKER, R. L. ENG, J. W. GASHWILER, AND M. H. SCHROEDER. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88: 165-171.

BUNTING, S. C., B. M. KILGORE, AND C. L. BUSHEY. 1987. Guidelines for prescribed burning sagebrush-grass rangelands in the northern great basin. United States Department of Agriculture, Forest Service, General Technical Report INT-231, Ogden, Utah, USA.

CALL, M. W., AND C. MASER. 1985. Wildlife habitats in managed rangelands—the great basin of southeastern Oregon. Sage grouse. United States Department of Agriculture, Forest Service, General Technical Report PNW-187, Portland, Oregon, USA.

COGGINS, K. A. 1998. Sage grouse habitat use during the breeding season on Hart Mountain National Antelope Refuge. Thesis, Oregon State University, Corvallis, USA.

COMMONS, M. L., R. K. BAYDACK, AND C. E. BRAUN. 1999. Sage grouse response to pinyon-juniper management. Pages 238-239 *in* S. B. Monson and R. Stevens, compilers. Proceedings: ecology and management of pinyon-juniper communities. United States Department of Agriculture, Forest Service, RMRS-P9, Fort Collins, Colorado, USA.

CONNELLY, J. W., JR. 1982. An ecological study of sage grouse in southeastern Idaho. Dissertation, Washington State University, Pullman, USA.

CONNELLY, J. W., W. J. ARTHUR, AND O. D. MARKHAM. 1981. Sage grouse leks on recently disturbed sites. Journal of Range Management 52: 153-154.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000*a*. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6: in press.

CONNELLY, J. W., AND C. E. BRAUN. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3/4: 123-128.

CONNELLY, J. W., H. W. BROWERS, AND R. J. GATES. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52: 116-122.

CONNELLY, J. W., AND L. A. DOUGHTY. 1989. Sage grouse use of wildlife water developments in southeastern Idaho. Pages 167-173 *in* S. Stiver and G. Tsukomoto, editors. Symposium on wildlife water developments. Nevada Department of Fish and Game, Reno, USA.

CONNELLY, J. W., R. A. FISCHER, A. D. APA, K. P. REESE, AND W. L. WAKKINEN. 1993. Renesting of sage grouse in southeastern Idaho. Condor 95: 1041-1043.

CONNELLY, J. W., AND O. D. MARKHAM. 1983. Movements and radionuclide concentrations of sage grouse in southeastern Idaho. Journal of Wildlife Management 47: 169-177.

CONNELLY, J. W., K. P. REESE, R. A. FISCHER, AND W. L. WAKKINEN. 2000*b*. Response of sage grouse breeding population to fire in southeastern Idaho. Wildlife Society Bulletin 28: 90-96.

CONNELLY, J. W., K. P. REESE, W. L. WAKKINEN, M. D. ROBERTSON, AND R. A. FISCHER. 1994. Sage grouse ecology report. Idaho Department of Fish and Game, Job Completion Report W-160-R-19, Subproject 9, Boise, Idaho, USA.

CONNELLY, J. W., W. L. WAKKINEN, A. D. APA, AND K. P. REESE. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55: 521-524.

COWLISHAW, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conservation Biology 13: 1183-1193.

DALKE, P. D., D. B. PYRAH, D. C. STANTON, J. E. CRAWFORD, AND E. F. SCHLATTERER. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27: 810-841.

DELONG, A. K. 1993. Relationships between vegetative structure and predation rates of artificial sage grouse nests. Thesis,

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Oregon State University, Corvallis, USA.

DeLong, A. K., J. A. Crawford, and D. C. DeLong, Jr. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59:88-92.

Dobkin, D. S. 1995. Management and conservation of sage grouse, denominative species for the ecological health of shrubsteppe ecosystems. United States Department of Interior, Bureau of Land Management, Portland, Oregon, USA.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994*a*. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54: 170-176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994*b*. Diets and food selection of sage grouse chicks in Oregon. Journal of Range Management 47:90-93.

Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile sage grouse. Journal of Wildlife Management 50:228-235.

Edelmann, F. B., M. J. Ulliman, M. J. Wisdom, K. P. Reese, and J. W. Connelly. 1998. Assessing habitat quality using population fitness parameters: a remote sensing-GIS-based habitat-explicit population model for sage grouse (*Centrocercus urophasianus*). Idaho Forest, Wildlife and Range Experiment Station, Technical Report 25, Moscow, USA.

Edminster, F. C. 1954. American game birds of field and forest. Charles Scribner's Sons, New York, New York, USA.

Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023-1028.

Eng, R. L. 1963. Observations on the breeding biology of male sage grouse. Journal of Wildlife Management 27:841-846.

Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. Journal of Wildlife Management 36:141-146.

Eng, R. L., E. J. Pitcher, S. J. Scott, and R. J. Greene. 1979. Minimizing the effect of surface coal mining on a sage grouse population by a directed shift of breeding activities. Pages 464-468 *in* G. A. Swanson, technical coordinator. The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats. United States Department of Agriculture, Forest Service, General Technical Report RM-65, Fort Collins, Colorado, USA.

Enyeart, G. 1956. Responses of sage grouse to grass reseeding in the Pines area, Garfield County, Utah. Thesis, Utah State Agricultural College, Logan, USA.

Fischer, R. A. 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. Dissertation, University of Idaho, Moscow, USA.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038-1041.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996*a*. An investigation on fire effects within xeric sage grouse brood habitat. Journal of Range Management 49:194-198.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996*b*. Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. Condor 98:868-872.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1997. Effects of prescribed fire on movements of female sage grouse from breeding to summer ranges. Wilson Bulletin 109:82-91.

Flinders, J. T. 1999. Restoration of sage grouse in Strawberry Valley, Utah, 1998-99 report. Utah Reclamation Mitigation and Conservation Commission, Progress Report. Brigham Young University, Provo, Utah, USA.

Gates, R. J. 1983. Sage grouse, lagomorph, and pronghorn use of a sagebrush grassland burn site on the Idaho National Engineering Laboratory. Thesis, Montana State University, Bozeman, USA.

Gates, R. J. 1985. Observations of the formation of a sage grouse lek. Wilson Bulletin 97:219-221.

Gill, R. B. 1965. Distribution and abundance of a population of sage grouse in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

Girard, G. L. 1937. Life history, habits, and food of the sage grouse, *Centrocercus urophasianus* Bonaparte. University of Wyoming, Publication 3, Laramie, USA.

Gratson, M. W., J. W. Unsworth, P. Zager, and L. Kuck. 1993. Initial experiences with adaptive resource management for determining appropriate antlerless elk harvest rates in Idaho. Transactions of the North American Wildlife and Natural Resources Conference 58:610-619.

Gray, G. M. 1967. An ecological study of sage grouse broods with reference to nesting, movements, food habits and sagebrush strip spraying in the Medicine Lodge drainage, Clark County, Idaho. Thesis, University of Idaho, Moscow, USA.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage grouse in Oregon. Thesis, Oregon State University, Corvallis, USA.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Hane, J. M., P. A. Schmidt, and E. B. Groshens. 1994. Sage grouse in the high desert of central Oregon: results of a study, 1988-1993. United States Department of Interior, Bureau of Land Management, Series P-SG-01, Prineville, Oregon, USA.

Heath, B. J., R. Straw, S. H. Anderson, and J. Lawson. 1997. Sage grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Project Completion Report, Laramie, USA.

Higby, L. W. 1969. A summary of the Longs Creek sagebrush control project. Proceedings, Biennial Western States Sage Grouse Workshop 6:164-168.

Hironaka, M., M. A. Fosberg, and A. H. Winward. 1983. Sagebrush-grass habitat types of southern Idaho. Idaho Forest, Wildlife and Range Experiment Station, Bulletin 35, Moscow, Idaho, USA.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Hornaday, W. T. 1916. Save the sage grouse from extinction, a demand from civilization to the western states. New York Zoological Park Bulletin 5:179-219.

Hulet, B. V. 1983. Selected responses of sage grouse to prescribed fire, predation, and grazing by domestic sheep in southeastern Idaho. Thesis, Brigham Young University, Provo, Utah, USA.

Hupp, J. W. 1987. Sage grouse resource exploitation and endogenous reserves in Colorado. Dissertation, Colorado State University, Fort Collins, USA.

Hupp, J. W., and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53:823-829.

Jenni, D. A., and J. E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring censuses. Journal of Wildlife Management 42:46-52.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

JOHNSON, K. H., AND C. E. BRAUN. 1999. Viability and conservation of an exploited sage grouse population. Conservation Biology 13:77-84.

KEISTER, G. P., AND M. J. WILLIS. 1986. Habitat selection and success of sage grouse hens while nesting and brooding. Oregon Department of Fish and Wildlife, Progress Report W-87-R-2, Subproject 285, Portland, Oregon, USA.

KLEBENOW, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649-661.

KLEBENOW, D. A. 1970. Sage grouse versus sagebrush control in Idaho. Journal of Range Management 23:396-400.

KLEBENOW, D. A. 1972. The habitat requirements of sage grouse and the role of fire in management. Tall Timbers Fire Ecology Conference 12:305-315.

KLOTT, J. H., AND F. G. LINDZEY. 1990. Brood habitats of sympatric sage grouse and Columbian sharp-tailed grouse in Wyoming. Journal of Wildlife Management 54:84-88.

KLOTT, J. H., R. B. SMITH, AND C. VULLO. 1993. Sage grouse habitat use in the Brown's Bench area of south-central Idaho. United States Department of Interior, Bureau of Land Management, Idaho State Office, Technical Bulletin 93-4, Boise, Idaho, USA.

LYON, A.G. 2000. The potential effects of natural gas development on sage grouse (*Centrocercus urophasianus*) near Pinedale, Wyoming. Thesis, University of Wyoming, Laramie, USA.

LEONARD, K. M., K. P. REESE, AND J. W. CONNELLY. 2000. Distribution, movements, and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6: in press.

MACK, R. N., AND J. N. THOMPSON. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119: 757-773.

MACNAB, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin 11:397-401.

MARTIN, N. S. 1970. Sagebrush control related to habitat and sage grouse occurrence. Journal of Wildlife Management 34: 313-320.

MARTIN, R. C. 1990. Sage grouse responses to wildfire in spring and summer habitats. Thesis, University of Idaho, Moscow, USA.

MCARTHUR, E. D., A. C. BLAUER, AND S. C. SANDERSON. 1988. Mule deer-induced mortality of mountain big sagebrush. Journal of Range Management 41:114-117.

MUSIL, D. D., J. W. CONNELLY, AND K. P. REESE. 1993. Movements, survival, and reproduction of sage grouse translocated into central Idaho. Journal of Wildlife Management 57:85-91.

MYERS, O. B. 1992. Sage grouse habitat enhancement: effects of sagebrush fertilization. Dissertation, Colorado State University, Fort Collins, USA.

NELLE, P. J. , K. P. REESE, AND J. W. CONNELLY. 2000. The long-term effect of fire on sage grouse nesting and brood-rearing habitats on the Upper Snake River Plain. Journal of Range Management 53:586-591.

OWENS, M. K., AND B. E. NORTON. 1992. Interactions of grazing and plant protection on basin big sagebrush (*Artemisia tridentata* spp. *tridentata*) seedling survival. Journal of Range Management 45:257-262.

OYLER-MCCANCE, S. J., N. W. KAHN, K. P. BURNHAM, C. E. BRAUN, AND T. W. QUINN. 1999. A population genetic comparison of large and small-bodied sage grouse in Colorado using microsatellite and mitochondrial DNA markers. Molecular Ecology, 8: 1457-1465.

PATTERSON, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado, USA.

PETERSEN, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

PETERSON, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147-155.

PETERSON, J. G. 1995. Ecological implications of sagebrush manipulation: a literature review. Montana Fish, Wildlife, and Parks, Helena, USA.

PYLE, W. H., AND J. A. CRAWFORD. 1996. Availability of foods of sage grouse chicks following prescribed fire in sagebrush-bitterbrush. Journal of Range Management 49:320-324.

PYRAH, D. B. 1972. Effects of chemical and mechanical sagebrush control on sage grouse. Montana Fish and Game Department, Job Completion Report W-105-R-6, Helena, USA.

REESE, K. P., AND J. W. CONNELLY. 1997. Translocations of sage grouse *Centrocercus urophasianus* in North America. Wildlife Biology 3/4:235-241.

REMINGTON, T. E., AND C. E. BRAUN. 1985. Sage grouse food selection in winter, North Park, Colorado. Journal of Wildlife Management 49:1055-1061.

REMINGTON, T. E., AND C. E. BRAUN. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

ROBERTSON, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southeastern Idaho. Thesis, University of Idaho, Moscow, USA.

ROGERS, G. E. 1964. Sage grouse investigations in Colorado. Colorado Game, Fish, and Parks Department, Technical Publication 16, Denver, Colorado, USA.

SAAB, V. A., AND T. D. RICH. 1997. Large-scale conservation assessment for neotropical migratory land birds in the interior Columbia River Basin. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-399, Portland, Oregon, USA.

SAUER, J. R., J. E. HINES, J. FALLON AND G. GOUGH. 1997. The North American breeding bird survey, results and analysis 1996-98. Version 98.1. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

SAVAGE, D. E. 1969. Relation of sage grouse to upland meadows in Nevada. Nevada Fish and Game Commission, Job Completion Report, Project W-39-R-9, Job 12, Reno, Nevada, USA.

SCHOENBERG, T. J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

SCHROEDER, M. A. 1995. Productivity and habitat use of sage grouse in north-central Washington. Washington Department of Fish and Wildlife, Job Progress Report Project W-96-R, Olympia, USA.

SCHROEDER, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The birds of North America, No. 425. The Birds of North America, Philadelphia, Pennsylvania, USA.

SIME, C. A. 1991. Sage grouse use of burned, non-burned, and seeded vegetation communities on the Idaho National

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

Engineering Laboratory, Idaho. Thesis, Montana State University, Bozeman, USA.

SVEUM, C. M. 1995. Habitat selection by sage grouse hens during the breeding season in south-central Washington. Thesis, Oregon State University, Corvallis, USA.

SVEUM, C. M., W. D. EDGE, AND J. A. CRAWFORD. 1998*a*. Nesting habitat selection by sage grouse in south-central Washington. Journal of Range Management 51:265-269.

SVEUM, C. M., J. A. CRAWFORD, AND W. D. EDGE. 1998*b*. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58:344-351.

SWENSON, J. E. 1986. Differential survival by sex in juvenile sage grouse and gray partridge. Ornis Scandinavica 17:14-17.

SWENSON, J. E., C. A. SIMMONS, AND C. D. EUSTACE. 1987. Decrease of sage grouse *Centrocercus urophasianus* after plowing of sagebrush steppe. Biological Conservation 41:125-132.

TATE, J., JR., M. S. BOYCE, AND T. R. SMITH. 1979. Response of sage grouse to artificially created display ground. Pages 464-468 *in* G. A. Swanson, technical coordinator. The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats. United States Department of Agriculture, Forest Service, General Technical Report RM-65, Fort Collins, Colorado, USA.

TISDALE, E. W., AND M. HIRONAKA. 1981. The sagebrush-grass region: a review of the ecological literature. Idaho Forest, Wildlife, and Range Experiment Station, Bulletin 33, Moscow, USA.

TRUEBLOOD, R. W. 1954. The effect of grass reseeding in sagebrush lands on sage grouse populations. Thesis, Utah State Agricultural College, Logan, USA.

VALE, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. Journal of Range Management 28:32-36.

VALLENTINE, J. F. 1989. Range development and improvements. Third edition. Academic, San Diego, California, USA.

VALLENTINE, J. F. 1990. Grazing management. Academic, San Diego, California, USA.

WAKKINEN, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. Thesis, University of Idaho, Moscow, USA.

WAKKINEN, W. L., K. P. REESE, AND J. W. CONNELLY. 1992. Sage grouse nest locations in relation to leks. Journal of Wildlife Management 56:381-383.

WALLESTAD, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129-136.

WALLESTAD, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Fish and Game Department, Technical Bulletin, Helena, USA.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630-633.

WALLESTAD, R. O., AND P. SCHLADWEILLER. 1974. Breeding season movements and habitat selection of male sage grouse. Journal of Wildlife Management 38:634-637.

WALLESTAD, R. O., J. G. PETERSON, AND R. L. ENG. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39:628-630.

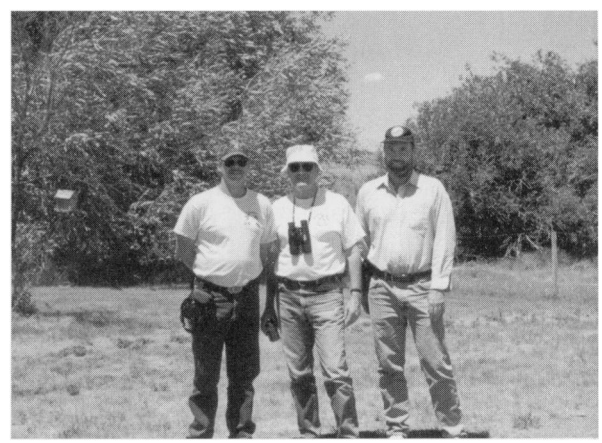
WAMBOLT, C. L., AND G. F. PAYNE. 1986. An 18-year comparison of control methods for Wyoming big sagebrush in southwestern Montana. Journal of Range Management 39:314-319.

WELCH, B. L., J. C. PEDERSON, AND R. L. RODRIQUEZ. 1988. Selection of big sagebrush by sage grouse. Great Basin Naturalist 48:274-279.

WELCH, B. L., F. J. WAGSTAFF, AND J. A. ROBERSON. 1991. Preference of wintering sage grouse for big sagebrush. Journal of Range Management 44:462-465.

YOUNG, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. Dissertation, Purdue University, West Lafayette, Indiana, USA.

ZABLAN, M. A. 1993. Evaluation of sage grouse banding program in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.



John W. (Jack) Connelly (left) is a wildlife research biologist with the Idaho Department of Fish and Game. He received his B.S. in fish and wildlife resources from the University of Idaho and M.S. in wildlife biology and Ph.D. in zoology from Washington State University. He has been a member of The Wildlife Society for 25 years and is past-president of the Idaho Chapter and current president of the Northwest Section. He has been involved with research on sage grouse since 1977. ***Michael A. (Mike) Schroeder*** (right) is the upland bird research biologist for the Washington Department of Fish and Wildlife. He received his B.S. in wildlife ecology from Texas A&M University, M.S. in zoology from the University of Alberta, and Ph.D. in wildlife biology from Colorado State University. He has been a member of The Wildlife Society for 21 years. He has been studying Washington populations of sage grouse, sharp-tailed grouse, and spruce grouse since 1992. ***Alan R. Sands*** retired after 21 years as a wildlife biologist for the Bureau of Land Management and is now employed by The Nature Conservancy as a field representative for southwestern Idaho. He received his B.A. in math and science from San Diego State University and M.S. in wildlife management from Humboldt State University. He has been a member of The Wildlife Society for 25 years and is past vice-president of the Idaho Chapter. ***Clait E. Braun*** (center) recently retired from the Colorado Division of Wildlife. He received his B.S. in soil science from Kansas State University, M.S. from the University of Montana in forest wildlife management, and Ph.D. from Colorado State University in wildlife biology. He has been a member of The Wildlife Society for 39 years and is past-editor of *The Journal of Wildlife Management*, past-president of the Central Mountain and Plains Section, past Council Member, and past-president of The Wildlife Society.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:10:55 UTC
All use subject to http://about.jstor.org/terms

J. Range Manage.
57: 2-19 January 2004

Synthesis Paper

Ecology and management of sage-grouse and sage-grouse habitat

JOHN A. CRAWFORD, RICH A. OLSON, NEIL E. WEST, JEFFREY C. MOSLEY, MICHAEL A. SCHROEDER, TOM D. WHITSON, RICHARD F. MILLER, MICHAEL A. GREGG, AND CHAD S. BOYD

Authors are Professor, Department of Fisheries and Wildlife, Oregon State University, Nash Hall 104 Corvallis, Ore., 97331-3803; Professor, Department of Renewable Resources, University of Wyoming, Box 3354, Laramie, Wyo. 82701-3354; Professor, Department of Forest, Range, and Wildlife Sciences, Utah State University, Logan, Utah, 84322-5230; Professor, Department of Animal and Range Sciences, Montana State University, Bozeman, Mont. 59717-2820; Research Biologist, Washington Department of Fish and Wildlife, Bridgeport, Wash. 98813; Professor, Department of Plant Sciences, University of Wyoming, 747 Road 9, Powell, Wyo. 82435-9135; Professor, Department of Rangeland Resources, Oregon State University, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, Ore. 97720; Biologist, US Fish and Wildlife Service, Sheldon-Hart Mountain Refuges, P.O. Box 111, 18 South G Street, Lakeview, Ore. 97630; Rangeland Scientist, U.S.D.A.-ARS, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, Ore. 97720.

Abstract

Sage-grouse (*Centrocercus urophasianus* and *C. minimus*) historically inhabited much of the sagebrush-dominated habitat of North America. Today, sage-grouse populations are declining throughout most of their range. Population dynamics of sage-grouse are marked by strong cyclic behavior. Adult survival is high, but is offset by low juvenile survival, resulting in low productivity. Habitat for sage-grouse varies strongly by life-history stage. Critical habitat components include adequate canopy cover of tall grasses (≥ 18 cm) and medium height shrubs (40–80 cm) for nesting, abundant forbs and insects for brood rearing, and availability of herbaceous riparian species for late-growing season foraging. Fire ecology of sage-grouse habitat changed dramatically with European settlement. In high elevation sagebrush habitat, fire return intervals have increased (from 12–24 to > 50 years) resulting in invasion of conifers and a consequent loss of understory herbaceous and shrub canopy cover. In lower elevation sagebrush habitat, fire return intervals have decreased dramatically (from 50–100 to < 10 years) due to invasion by annual grasses, causing loss of perennial bunchgrasses and shrubs. Livestock grazing can have negative or positive impacts on sage-grouse habitat depending on the timing and intensity of grazing, and which habitat element is being considered. Early season light to moderate grazing can promote forb abundance/availability in both upland and riparian habitats. Heavier levels of utilization decrease herbaceous cover, and may promote invasion by undesirable species. At rates intended to produce high sagebrush kill, herbicide-based control of big sagebrush may result in decreased habitat quality for sage-grouse. Light applications of tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) can decrease canopy cover of sagebrush and increase grass and forb production which may be locally important to nesting

Resumen

El "Sage-grouse" (*Centrocercus urophasianus* and *C. minimus*) históricamente habitó gran parte del hábitat dominado por "Sagebrush" de Norteamérica. Actualmente, las poblaciones de "Sage-grouse" están disminuyendo a través de la mayor parte de su rango de adaptación. Las dinámicas de población del "Sage-grouse" están marcadas por un comportamiento fuertemente cíclico. La supervivencia de adultos es alta, pero es anulada por la baja supervivencia juvenil, resultando en una baja productividad. El hábitat del "Sage-grouse" varía fuertemente con la etapa de la historia de vida. Los componentes críticos de hábitat incluyen una adecuada cobertura de copa de zactaes altos (>18 cm) y arbustos medianos (40-80 cm) para anidar, abundantes hierbas e insectos para criar la camada y disponibilidad de hierbas ribereñas para el forrajea a finales de la estación de crecimiento. La ecología del fuego del hábitat del "Sage-grouse" cambio dramáticamente con la con la colonización europea. El las altas elevaciones del hábitat de "Sagebrush", los intervalos de retorno del fuego ha incrementado (de 12 - 24 a >50 años) resultando en una invasión de coníferas y una consecuente perdida del estrato herbáceo y de la cobertura de arbustos. En las bajas elevaciones del hábitat de "Sagebrush" los intervalos de retorno del fuego han disminuido (de 50 - 100 a <10 años) debido a la invasión de zacates anuales, causando una perdida de zacates perennes amacollados y arbustos. El apacentamiento del ganado puede tener impactos positivos o negativos en el hábitat del "Sage-grouse"dependiendo de la época e intensidad del apacentamiento y cual elemento del hábitat esta siendo considerado. A inicios de la estación el apacentamiento ligero a moderado puede promover la abundancia/disponibilidad de hierbas tanto en los hábitats de tierras altas como en los ribereños. Niveles fuertes de utilización disminuyen la cobertura de herbáceas y puede promover la invasión de especies indeseables. A las tasas con las que se intenta producir una alta muerte de "Sagebrush", el control del "Big sagebrush" basado en herbicidas puede resultar en una disminución de la calidad del hábitat para el "Sage-grouse". Aplicaciones ligeras de tebuthiuron (N-[5-(1,1-dimetiletil)-1,3,4-tiadiazol-2-yl]-N,N'-dimetilurea) puede disminuir la cobertura de "Sagebrush" e incrementar la producción de zacates y hierbas lo cual puede ser localmente importantes para las actividades de anidamiento y forrajeo. La capacidad de los mane-

This project was initiated by the Society for Range Management Wildlife Habitat Committee. Larry Rittenhouse provided comments and suggestions for the initial outline and Tim Westfall provided suggestions on content, helped assemble the team of authors, and provided insightful comments on portions of an earlier draft of the manuscript.

Authors are listed in order of random draw.

Corresponding author is Chad S. Boyd.

Manuscript accepted 20 Sept. 03.

026500

and foraging activities. The ability of resource managers to address sage-grouse habitat concerns at large scales is aided greatly by geomatics technology and advances in landscape ecology. These tools allow unprecedented linkage of habitat and population dynamics data over space and time and can be used to retroactively assess such relationships using archived imagery. The present sage-grouse decline is a complex issue that is likely associated with multiple causative factors. Solving management issues associated with the decline will require unprecedented cooperation among wildlife biology, range science, and other professional disciplines.

escala del hábitat del "Sage-grouse" es auxiliada grandemente por la tecnología geomática y los avances en la ecología de paisaje. Estas herramientas permiten un enlace sin precedentes entre los datos del hábitat y las dinámicas de la población a través del espacio y tiempo y pueden ser usadas retroactivamente para evaluar tales relaciones utilizando las imágenes archivadas. La disminución presente del "Sage-grouse" es un problema complejo que probablemente esta asociado con múltiples factores causales. La resolución de los problemas de manejo asociados con la diminución requerirá una cooperación sin precedentes entre las ciencias de biología de fauna silvestre, manejo de pastizales y otras disciplinas profesionales.

Key Words: population dynamics, habitat, fire ecology, livestock grazing, herbicide, landscape ecology

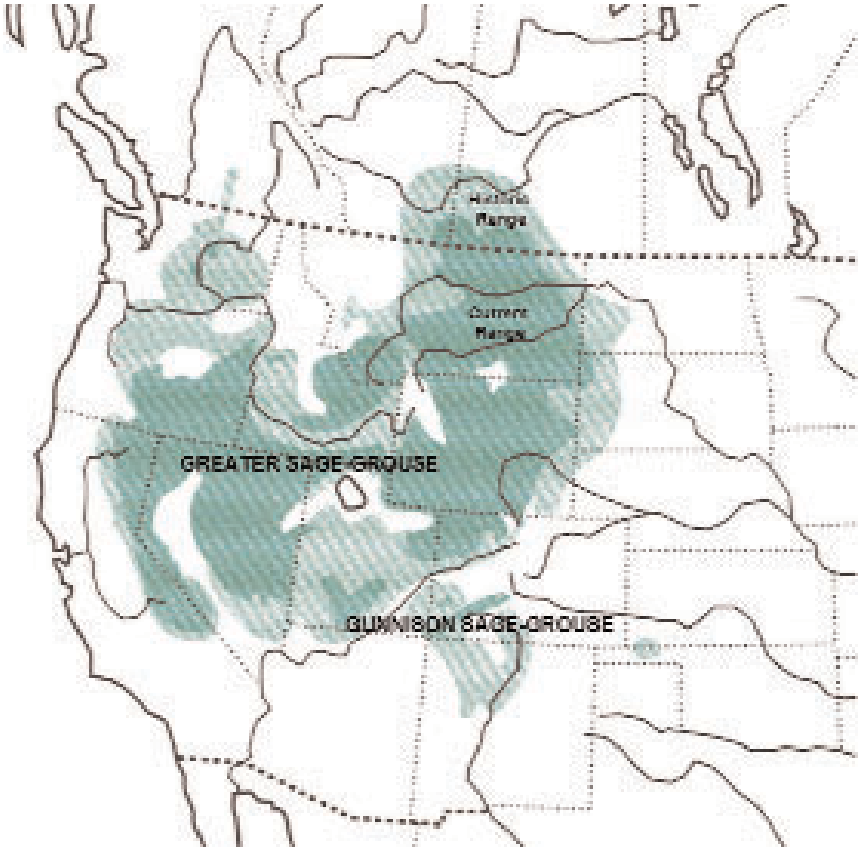


Fig. 1. Historical (light shading) and current (dark shading) range of greater (*Centrocercus urophasianus*) and Gunnison (*C. minimus*) sage-grouse. Gunnison sage grouse historically occurred in Oklahoma, Colorado, and Kansas, and are currently found south of Eagle River in Colorado. Adapted from Shroeder et al. (1999) and courtesy of A. Poole and F. Gill (eds.) The Birds of North America. 1999.

Historically, greater (*Centrocercus urophasianus*) and Gunnison (*C. minimus*) sage-grouse inhabited large portions of sagebrush-dominated North American rangelands [both sagebrush steppe and sagebrush semi-desert plant assemblages (West 1983a, 1983b, West and Young 2000)]. The subfamily Tetraoninae is reported to be of North American origin (Lucchini et al. 2001), and at one time, the range of sage-grouse encompassed significant portions of the western (US) states and extended north into the Canadian provinces of British Columbia, Alberta, and Saskatchewan (Fig. 1). Many plant communities providing habitat to sage-grouse have undergone significant, and in some cases, lasting changes in the 19th and 20th centuries. Factors responsible for plant community change have included (but are not limited to) alterations in fire regime; excessive livestock grazing; proliferation of non-native plant species; conversion of rangeland to seeded pastures [e.g. crested wheatgrass (*Agropyron cristatum* L.)], cropland and roads; and other land alterations. Concurrent with these habitat changes has been a generalized decline in sage-grouse abundance. The reasons for this decline are difficult to understand. Putting together the pieces of the puzzle involves integrating sage-grouse population ecology and habitat requirements, as well as the ecology and management of plant communities that comprise sage-grouse habitat. It is critical that the relationship between changes in habitat, and changes in sage-grouse populations be defined at multiple scales, given the extended temporal and spatial horizons that frame the ecology of these species.

This paper synthesizes current knowledge regarding pertinent topics in sage-grouse ecology and management and suggests direction for future research and management. Others (Braun et al. 1977, Beck and Mitchell 2000, Connelly et al. 2000, Rowland and Wisdom 2002) have provided synthesis and review papers previously. Our effort is not comprehensive to all factors affecting sage-grouse, but is meant to provide expanded coverage of topical management concerns with an emphasis on habitat ecology.

Population ecology

Connelly and Braun (1997) estimate a 17–47% decline in sage-grouse breeding populations since 1985 in states that have sufficient records for quantifying sage-grouse numbers. For many years periodic fluctuations in abundance were attributed to cycles, often over 8–12 year intervals (Batterson and Morse 1948, Rich 1985). Nevertheless, an explanation for fluctuations in abundance has been difficult to support with documented causal relationships (Braun 1998). Although the mechanisms underlying fluctuations in abundance

026501

Table 1. Range-wide averages for demographic parameters associated with population dynamics of greater (*Centrocercus urophasianus*) and Gunnison (*C.minimus*) sage-grouse in North America (Rasmussen and Griner 1938, Bean 1941, Keller et al. 1941, Batterson and Morse 1948, Patterson 1952, Nelson 1955, June 1963, Wallestad and Pyrah 1974, Wallestad 1975, Petersen 1980, Wakkinen 1990, Connelly et al. 1993, 1994, Zablan 1993, Gregg et al. 1994, Hanf et al. 1994, Young 1994, Schroeder 1997, Sveum et al. 1998a, 1998b, Schroeder et al. 1999, Aldridge 2000).

Parameter	Greater sage-grouse $\bar{x}$	n	Gunnison sage-grouse $\bar{x}$	n
Clutch size	7.5 eggs	10 studies	6.8 eggs	1 study
Hatchability	94.3%	8 studies		
Nest likelihood[a]	80.8%	7 studies	75.7%	1 study
Renest likelihood[b]	32.5%	7 studies	4.8%	1 study
Nest success[c]	47.4%	14 studies	43.2%	1 study
Annual reproductive success[d]	44.6%	8 studies	35.1%	1 study
Annual survival of breeding-aged males	48.9%	5 studies		
Annual survival of breeding-aged females	60.6%	6 studies		
Survival of juveniles[e]	10.0%	3 studies		

[a]The proportion of females attempting to nest.
[b]The propotion of females attempting to renest following their first nest failure.
[c]The probability of a single nest hatching ≥ 1 egg.
[d]The probability of a female hatching ≥ 1 egg in a season.
[e]Approximate estimate of survival to the first potential breeding season based on partial estimates from 3 studies.

are still debated, the major concern now is that most (but not all) populations are showing long-term declines, whether cyclic in the short-term or not (Braun 1998).

Productivity, survival and recruitment

The dynamics of a population are a reflection of productivity, survival, and recruitment. Productivity can be further divided into stages, including clutch size, hatchability, nest likelihood, renest likelihood, nest success, and annual reproductive success (Schroeder et al. 1999; Table 1). Sage-grouse productivity is low, despite their high reproductive potential. Declines in productivity appear to be related to a substantial number of non-nesting females (nest/renest likelihood in Table 1) and low rate of annual reproductive success. Nest success is inversely correlated with density of predators, such as common ravens (*Corvus corax*, Batterson and Morse 1948), however, rates of predation are tied to habitat quality, and it has been suggested that the most efficient method for mitigating high rates of nest predation may be through the effective management of habitat (Hamerstrom et al. 1957, Angelstam 1986, Andrén and Angelstam 1988, Schroeder and Baydack 2001). The impact of re-nesting on productivity is unclear; renesting has had limited impact on overall productivity in Oregon (Gregg et al. 1994, Hanf et al. 1994) and Idaho (Connelly et al. 1993), however, Schroeder (1997) reported that 38% of productivity in north-central Washington was due to re-nesting.

Productivity, and subsequently recruitment, is further impacted by low juvenile survival rates between hatch and the following breeding season (Table 1). Juvenile survival has proven difficult to document in the field but the available estimates for this parameter are very low, suggesting that understanding juvenile survival may be critical in managing the population dynamics of sage-grouse. Food availability (Pyle and Crawford 1996), habitat quality (Sveum et al. 1998a), harvest (Crawford and Lutz 1985), predation (Batterson and Morse 1948), and weather (Blake 1970, Rich 1985) all affect juvenile survival. Recruitment of young birds into the breeding population may be further complicated by dispersal of juveniles from the nesting location (Browers and Flake 1985, Dunn and Braun 1985, 1986). The direct impact of dispersal on population dynamics of sage-grouse remains largely unexplored.

In contrast to low nest success and low survival of juveniles, annual survival of breeding-aged birds tends to be higher than 50% in most situations, and as high as 75% for breeding-aged females in Idaho (Connelly et al. 1994). Although high adult survival rates may compensate for low productivity, it has been insufficient to reverse their widespread declines in abundance (Braun 1998).

Population fluctuations and research needs

The relatively high survival rates and low productivity of adult sage-grouse may help explain the dramatic fluctuations in sage-grouse abundance that some have suggested resemble "cycles" (Rich 1985). Although sage-grouse have a high reproductive potential, they may only rarely have years where productivity is high. These infrequent "boom" years, in combination with the high survival of breeding-aged birds, may produce multi-year fluctuations in abundance.

Dramatic fluctuations in abundance (Rich 1985) create tremendous problems for evaluating population-level responses to management. For example, although habitat quality is related to sage-grouse population dynamics (Edelmann et al. 1998), there are 4 basic reasons why most management changes require years before a population change is detected. First, changes in habitat management do not immediately alter habitat characteristics. This is particularly true where habitat has undergone gradual, long-term structural and/or compositional changes. Second, sage-grouse population response may lag behind changes in sage-grouse productivity. This lag effect occurs because yearling males may not display on leks (Jenni and Hartzler 1978, Emmons and Braun 1984) and yearling females may not nest (Connelly et al. 1993, Gregg et al. 1994) during their first potential breeding season. Third, population responses to short-term habitat management (< 10 years) may not be observed in sage-grouse populations, because the typical fluctuations in a 10-year interval may dwarf any response to improved management. Fourth, the lack of basic information on important stages in the life history of sage-grouse, such as juvenile survival, may indicate that the appropriate habitat management strategy for a given population is not yet known.

Habitat management is one of the few areas where research has shown that reproductive parameters can be altered. For example, substantial data exists documenting significant relationships between specific habitat characteristics and annual reproductive success (Bean 1941, Pyrah 1971, Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, Hanf et al. 1994, Young 1994, DeLong et al. 1995, Sveum et al. 1998b). Adequate habitat provides the cover necessary to conceal nests and provides the foods necessary for hens to lay eggs and incubate clutches (Barnett and Crawford 1994). Manipulation of habitat also has potential to influence other aspects of sage-grouse population dynamics including clutch size, nest and renest likelihood, and survival of juveniles and breeding-aged birds. For example, adequate vegetational canopy cover may pro-

026502

vide critical escape cover, thus lowering the risk of predation.

Although many of the specific relationships between habitat quality and productivity and survival are not clear, the overall relationship can be illustrated by the dramatic changes in landscape throughout the historical North American range of sage-grouse. Most remaining populations are associated with intact habitats in relatively northern latitudes, high elevations, and/or mesic environments (Connelly and Braun 1997). In contrast, significantly altered habitats and those in southern latitudes, low elevations, and/or xeric environments have become uninhabitable. This is a trend that has been ongoing for the past 100 years and is likely to continue unless there are widespread changes in management (Brown and Davis 1995). In addition, the continued reduction in occupied habitat will result in increased fragmentation and isolation of remaining sage-grouse populations.

Although a substantial quantity of data exists on some basic parameters associated with population dynamics (e.g., clutch size, egg hatchability, nesting success, survival of breeding age birds), information on juvenile survival, dispersal, and recruitment is inadequate. It is essential that research be initiated as soon as possible, because of the dramatic declines in sage-grouse distribution and abundance (Connelly and Braun 1997, Braun 1998) and because of the long time periods (> 10 years) needed to observe treatment effects in a species with low productivity and high survival. It is also critical that other research continues, including the influence of nutrition (Barnett and Crawford 1994, Pyle and Crawford 1996), weather (Gill 1966, Blake 1970, Hupp and Braun 1989), predation (Batterson and Morse 1948, Schroeder and Baydack 2001), and behavior (Scott 1942, Gibson and Bradbury 1986) on population dynamics.

Sage-grouse habitat relationships

While many factors likely influence productivity, the only factor that has been consistently manageable is habitat (Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998b). The importance of sagebrush (woody *Artemisia*) as a source of cover and food for sage-grouse is well known (Patterson 1952, Braun et al. 1977), however, sage-grouse require a variety of plant community types for breeding, nesting, brood-rearing and wintering (Table 2). Describing habitat relationships is complicated by the fact that sage-grouse populations often display complex seasonal movement patterns. Populations may exhibit different patterns of migration, with some populations remaining resident throughout the year, some migrating between wintering and breeding habitat, and some with more complicated movements (Connelly et al. 1988). Migratory birds in Idaho have been reported to range up to 125 km, with an annual home range size of 2,764 km^2 (Leonard et al. 2000). For management purposes, spatial patterns of habitat use over time should be determined on a population-by-population basis.

Winter habitat

During winter, sage-grouse utilize medium to tall sagebrush communities (25–80 cm, or 25–35 cm above the snow) on south and west facing slopes (Ihli et al. 1973, Connelly et al. 2000; Table 2), and forage primarily on sagebrush leaves (Patterson 1952). Where available, low sagebrush (*A. arbuscula* Nutt.) habitat (particularly on wind-swept ridges) is also used (Hanf et al. 1994). Home range for wintering migratory and non-migratory populations has been reported as > 140 km^2 (Robertson 1991) and 11 to 31 km^2 (Wallestad 1975), respectively. Sagebrush canopy cover at sage-grouse winter use sites can range from 12% in Oregon (Hanf et al. 1994) to 43% in Colorado (Schoenberg 1982), but adequate cover is typically available on a landscape scale (Connelly et al. 2000). Unless snow completely covers sagebrush (Hupp and Braun 1989), severe winter weather conditions have little effect on sage-grouse populations (Call and Maser 1985) and sage-grouse may actually gain weight during the winter months (Beck and Braun 1978).

Table 2. Sage grouse habitat/reproductive parameters and key plant community and dietary/structural components (Ihli et al. 1973, Hulet et al. 1986, Gregg et al. 1993, 1994, Barnett and Crawford 1994, Drut et al. 1994a, 1994b, Delong et al. 1995, Sveum et al. 1998a, 1998b, Schroeder et al. 1999, Connelly et al. 2000, Aldridge and Brigham 2002).

Habitat/reproductive parameter	Plant community type	Important dietary/structural components
Winter	Big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Welsh and ssp. vaseyana Rydb.) but other species may be used (e.g. *A. arbuscula* Nutt., *A. cana* Pursh)	Medium height (25-80 cm) and taller sagebrush on south and west exposures, windswept low sagebrush
Lekking	Sparsely vegetated areas on ridgetops, swales, and dry lakebeds (burned areas, grassy meadows, plowed fields, or cleared roadsides may also be used)	Low or absent vegetation canopy (0.04 ha to 4 ha in size) within sagebrush sites
Pre-laying: Nest and renest initiation	Low sagebrush (*A. arbuscula, A nova* A. Nels., *A. rigida* Nutt.) and Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*)	Key forbs (legumes and composites) and sagebrush
Nesting: Nest and renest success	Sagebrush (*A. arbuscula, A. cana, A. tridentata*. ssp. *wyomingensis and vaseyana, A. tripartita* Rydb.), bitterbrush (*Purshia tridentata* Pursh DC.) and rabbitbrush (*Chrysothamnus* spp. Nutt.)	Tall (> 18 cm) residual bunchgrass cover, medium height shrubs (40–80 cm)
Brood-rearing: Chick survival and recruitment	Big and low sagebrush, riparian habitat	Key forbs (legumes and composites) and insects, succulent mesic vegetation and sagebrush
Broodless hens and males (growing season)	Big and low sagebrush, riparian habitat	Sagebrush, key forbs (legumes and composites) and insects

026503

Lekking habitat

Leks are typically located in sparsely vegetated areas (Call and Maser 1985) with few to 100 or more displaying males. Leks typically reflect the availability of nesting habitat in the surrounding area. There is no evidence that lek habitat is limiting to sage-grouse populations (Schroeder et al. 1999), and, if needed, lekking habitat can be created by management activity (Eng et al. 1979, Tate et al. 1979).

Pre-laying habitat

The pre-laying period is defined as the 5-week period preceding incubation (Barnett 1992) when habitat use centers around low sagebrush (*A. arbuscula* Nutt., but also, *A. nova* A. Nels. and *A. rigida* Nutt.) and Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Rydb.) communities (Table 2). During this period 50–80% of the hen's diet is sagebrush with the remainder being mostly forbs (Barnett and Crawford 1994). Although sagebrush leaves contribute importantly to the dry mass of the diet of pre-laying hens, the nutrient contribution of forbs overshadows that of sagebrush and may be associated with increased reproductive success (Barnett and Crawford 1994). Some authors (e.g., Rogers 1964, Patterson 1952, Wallestad et al. 1975) have reported that sagebrush comprises > 85% of the diet during the pre-laying period. However, these authors did not separate diets by sex.

Nesting habitat

Sage-grouse nests are typically located under sagebrush plants, often in mountain big sagebrush (*A. t.* ssp. *vaseyana* Rydb) habitat (Wallestad and Pyrah 1974, Gregg et al. 1994). A variety of other sagebrush-dominated community types as well as bitterbrush (*Purshia tridentata* Pursh DC.) and rabbitbrush (*Chrysothamnus* spp. Nutt.) sites may also be utilized (Hulet et al. 1986, Crawford et al. 1992, Aldridge and Brigham 2002; Table 2). Nests are generally located near leks, but hens may move long distances from leks to nest (Hanf et al. 1994). In Idaho, 55% of nests were within 3 km of the lek of capture (Wakkinen et al. 1992). Poor reproductive success may result from a lack of key structural habitat features necessary for nesting (Blake 1970, Autenrieth 1981). Nest site selection is largely a function of height and amount of shrub canopy cover (Klebenow 1969, Roberson 1986, Gregg 1992), while tall (> 18cm) residual bunchgrasses provide cover for screening (Gregg 1992, Gregg et al. 1994). Successful nests in Oregon had 41% canopy cover of medium height (40–80 cm) sagebrush and 18% tall bunchgrass (residual) canopy cover in the 3-m^2 area surrounding the nest (Gregg et al. 1994). Other forms of herbaceous vegetation (e.g., residual forbs) may provide nest screening cover (Sveum et al. 1998b), however, exotic invaders (e.g., cheatgrass *Bromus tectorum* L.) generally do not. Sagebrush canopy cover in nesting habitat should range from 15–25% (Connelly et al. 2000). Winward (1991) suggested that maximum understory herbaceous production would be realized at 12% sagebrush cover in Wyoming big sagebrush types and 20% sagebrush cover in mountain big sagebrush types.

The most common reason for nest failure is predation by coyotes (*Canis latrans*) and avian and small mammal species (Batterson and Morse 1948, Nelson 1955, Autenrieth 1981, DeLong 1994). However, adequate vegetation structure at the nest site provides visual, scent and physical barriers between ground nesting birds and predators, and may ultimately determine susceptibility to predation (Gregg 1992, Gregg et al. 1994). Canopy cover of tall grasses and medium height sagebrush is inversely related to the probability of nest predation in big sagebrush habitats (Connelly et al. 1991, Delong et al. 1995, Sveum et al. 1998b).

Brood-rearing habitat

The pattern of habitat use during the brood-rearing period is related to changes in food availability and hens with broods are typically found where forb abundance is greatest (Klebenow 1969, Drut et al. 1994a). For example, Sveum et al. (1998a) reported > 20% canopy cover of forbs at brood-rearing sites and decreased shrub canopy cover (14 vs. 20%) relative to random locations in Wyoming big sagebrush habitat. Specific habitats used during brood-rearing (Table 2) are more mesic as the growing season progresses, which is associated with forb desiccation (Wallestad 1971). Home range size for broods has been reported to range from less than 1 km^2 in Montana (Wallestad 1971) to 5 km^2 in Oregon (Drut et al. 1994a). Differences in home range size among broods have been attributed to availability of forbs (Drut et al. 1994a). Use of riparian habitat is dependent on desiccation of forbs in sagebrush uplands and may occur earlier in drought years (Savage 1969, Oakleaf 1971, Danvir 2002).

Forbs and insects comprise the bulk of sage-grouse chick diets until they are approximately 12 weeks of age, at which time sagebrush becomes a common component (Dargen et al. 1942, Nelson 1955, Klebenow and Gray 1968, Peterson 1970). Specific taxa consumed by chicks are very diverse. In Oregon chicks consumed 41 families of invertebrates, 34 genera of forbs, 2 genera of shrubs, and 1 genus of grass (Pyle 1993, Drut et al. 1994b), however, only a few specific taxa of forbs were preferentially selected (Drut et al. 1994b). The relationship between chick survival/recruitment and dietary factors has not been elucidated for most wild galliformes, especially the tetraonids (Potts 1986). However, data suggest that availability of forbs and invertebrates is associated positively with survival/recruitment of sage-grouse chicks (Drutt et al. 1994b). This relationship may be of particular importance during drought years when forb availability is low and sagebrush becomes a greater component of the chick diet at an earlier age (Drut et al. 1994a).

Broodless hens and male habitat (growing season)

Because sage-grouse nesting and brood-rearing success is extremely low in some years, a relatively large portion of the summer female sage-grouse population is composed of broodless hens (Gregg et al. 1993). Survival of these hens may be important to population maintenance. Broodless hens begin to form small flocks of 2-3 birds in mid-May which may increase in size to 25 hens by early June (Gregg et al. 1993). Habitat use is similar to that of hens with broods (Table 2), however, broodless hens move to riparian habitat earlier than hens with broods (Dalke et al. 1963, Martin 1976, Gregg et al. 1993). Males follow a similar pattern of habitat use, but typically remain in flocks separate from females.

Monitoring considerations and research needs

Monitoring sage-grouse habitat is complicated by the migratory behavior of sage-grouse populations, or segments of populations (Connelly et al. 2000). As such, monitoring efforts and habitat assessments require knowledge of both the spatial and temporal dynamics of migratory patterns. However, these patterns do not directly influence the specific seasonal, community-scale habitat needs of sage-grouse populations. At present, establishing vegetation monitoring transects and quantifying availability of key habitat components (Connelly et al. 2000 and

026504

Table 2), coupled with an estimate of reproductive parameters, provides the best measure of sage-grouse habitat quality. Because all reproductive parameters may be important, evaluation of sage-grouse habitat must consider all of the key habitat components. A deficiency in any 1 factor can reduce productivity and ultimately abundance of sage-grouse in a particular area. Different critical habitat factors may limit sage-grouse populations in different areas.

There is a strong need to develop a consistent monitoring approach that focuses on the vegetation elements most important to sage-grouse at local (e.g., nest site), community, and landscape scales. Research is also needed to refine our knowledge of the optimal balance of key components (i.e., shrubs, grasses, and forbs) within seasonal habitats, and the optimal juxtaposition and interspersion of habitats across the landscape. Not much is known about the habitat factors that influence juvenile survival. Previous research has identified availability of key forbs as an important factor influencing juvenile survival. Other factors that may influence juvenile survival include physiological condition of the hen before nesting, insect availability, and the influence of vegetation structure and composition on predation. Understanding the relationship between habitat variables and juvenile survival is vital to understanding long-term fluctuations of sage-grouse populations.

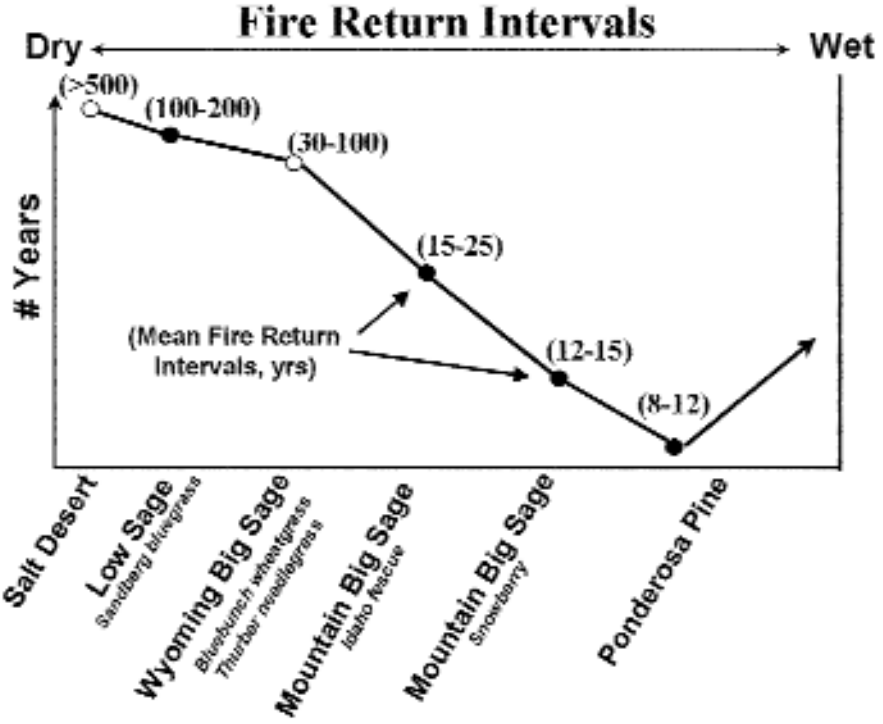


Fig. 2. Presettlement mean fire return intervals (MFRI) for salt desert, low sagebrush (*Artemisia arbuscula* Nutt.)/sandberg bluegrass (*Poa sandbergii* Vasey), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Welsh.)/bluebunch wheatgrass (*Agropyron spicatum* Pursh)/Thurber needlegrass (*Stipa thurberiana* Piper), mountain big sagebrush (*A.t.* ssp. *vaseyana* Rydb.)/Idaho fescue (*Festuca idahoensis* Elmer), mountain big sagebrush/snowberry (*Symphoricarpos* spp.), and ponderosa pine (*Pinus ponderosa* Laws.) communities. Solid circles are MFRI estimates supported by data, and open circles are estimates with little to no information [from Riegel et al. (in press)].

Impacts on sage-grouse habitat

European settlement precipitated significant ecological changes in the sagebrush region (Miller and Eddleman 2001). For example, West (1999a) estimated that 4.5 million hectares of sagebrush steppe have been converted to towns, communication corridors, or intensive agriculture. In the nonarable regions, a large portion of sagebrush-dominated communities has been altered by changes in the proportion of trees, shrubs, grasses, and forbs. Changes in structure and composition in non-cultivated areas are primarily attributed to altered fire regimes, improperly managed livestock grazing, introduction of exotic plants, and herbicide use (Miller et al. 1994).

Fire

Management of both wild and prescribed fires is considered one of the key issues in maintaining sage-grouse populations in sagebrush-dominated landscapes. Sage-grouse evolved in ecosystems where fire was a primary disturbance process. However, the role of fire in the sagebrush biome is often over generalized. Fire regimes are spatially complex and vary through time across the sagebrush region, and, since the 1860s, the ecological role of fire has changed dramatically (West 1983b, 2000, West and Young 2000, Miller and Tausch 2001).

Pre-European settlement

Presettlement fire return interval varied greatly depending on plant community type and moisture regime (Fig. 2). For example, mean fire return interval (MFRI = time between fires) varied between 12 and 25 years on productive mountain big sagebrush sites (Houston 1973, Burkhardt and Tisdale 1976, Gruell 1999, Miller and Rose 1999), but can exceed 200 years in more xeric mountain big sagebrush/western needlegrass (*Stipa occidentalis* Thurber) communities occupying sandy soils (Waichler et al. 2001, Miller unpublished data). Estimates of MFRI reported for Wyoming big sagebrush communities (Wright and Bailey 1982) are largely based on fuel loads and likely plant composition prior to settlement. However, MFRI only partially describes the frequency of fire. The variability of fire-free periods within a fire regime is very important in determining landscape plant community composition, structure, and fire behavior. Information on the variability of presettlement fire-free periods is limited. Two studies conducted in mountain big sagebrush communities where MFRI was relatively short (10 to 20 years) reported that presettlement fire-free periods varied between 8–29 years (Gruell 1999), and 3–28 years (Miller and Rose 1999). Fire size and complexity (patchiness) are also important factors influencing seed source for plant re-establishment (particularly sagebrush) and wildlife use patterns.

The response of presettlement communities following fire was largely determined by the preburn plant composition and fire tolerances of those species. Many herbaceous species in sage-grouse habitat are well adapted to fire (Blaisdell 1953, Wright and Klemmedson 1965, Conrad and Poulton 1966, Wright and Bailey 1982, Young and Miller 1985). Forb species that resprout belowground from a caudex, corm, bulb, rhizome, or rootstock,

026505

Table 3. Generalized response of forbs common to the sagebrush region to fire and herbicide (2,4-D) application (Blaisdell 1953, Pehanec et al. 1954, Payne 1973, Lyon and Stickney 1976, Klebenow and Beall 1977, Wright et al. 1979, Volland and Dell 1981, Blaisdell et al. 1982, Bradley et al. 1992).

Species	Fire	Herbicide 2,4-D
Achillea millifolium L.	O+	O-U+
Agoseris spp.	U	O
Allium accuminata Hook.	U	
Antennaria spp.	O-U	O
A. (mat spp.)	S	S
Aster spp.	U+	O-U+
Astragalus spp.	O-U	S-U
A. purshii Hook.	O	O
Balsomorhiza spp.	U+	S
Castilleja spp.	U	S
Crepis spp.	O+	U
Erigeron spp.	U	O
Eriogonum spp.	S	U
Geranium spp.	O+	O-U
Geum spp.	O-U	S
Lactuca serriola L.	O-U	O-U
Lomatium spp.	U	O
Lupinus spp.	U+	S
Mertensia spp.	O-U	S
Microsteris gracilis Hook.	U	O
Penstemon spp.	O	S-O
Phlox longifolia Nutt.	U+	O
P. hoodii Torry & A. Gray	S	O-U+
Potentilla spp.	U+	S-O
Senecio intergerrimus Nutt.	O	O
Solidago spp.	U	U
Taraxicum spp.	U	O
Tragopogon dubius Scop.	O	U+
Trifolium macrocephalum Pursh	U	S
Zigadenus paniculatus Nutt.		S

[a]S = Severely Damaged, O = Zero to Slight Damage, U = Undamaged, + = increases, - = declines.

exhibit rapid recovery following fire. Annual and biennial forbs usually increase following fire through seed dispersal mechanisms. However, forbs that are suffrutescent, low growing, or mat forming such as pussytoes (*Antennaria* spp. Gaertner) or several of the buckwheats (*Eriogonum* spp. Michx.) can be severely damaged by fire (Table 3). Big and low sagebrush and young juniper are easily killed by fire (Blaisdell 1953, Burkhardt and Tisdale 1976, Wright and Bailey 1982).

Reestablishment of sagebrush in burned sites is highly variable and dependent on nearby seed sources or seed reservoirs produced during the previous growing seasons in addition to weather conditions following the fire (West and Yorks 2002). Dispersal of sagebrush seed is limited to several meters from the parent plant. Reestablishment generally occurs more rapidly in the more mesic big sagebrush communities. Generally, shrub cover can reach or exceed preburn levels in as little as 20 years but more typically within 25–45 years (Watts and Wambolt 1996, Wambolt et al. 2001). A MFRI of less than 50 years in mountain big sagebrush communities and 100 years in low sagebrush/Sandberg bluegrass (*Poa sandbergii* Vasey) communities was sufficient to control the encroachment of pinyon or juniper (Burkhardt and Tisdale 1976, Miller and Rose 1999, Miller and Tausch 2001).

Post-European settlement

Two common scenarios of fire-related plant community change following European settlement are: 1) a decline in fire frequency resulting in increased dominance of woody species (shrubs or trees) and a decrease in perennial forbs and grasses; or 2) an increase in Eurasian weeds (particularly ephemerals), a consequent increase in fire frequencies, and loss of native perennial shrubs, forbs, and grasses (Fig. 3).

The first scenario represents one of the most significant losses in mountain big sagebrush habitat. For instance, Miller and Tausch (2001) estimated juniper and pinyon woodlands have increased 10-fold during the past 130 years from 2.9 to 29 million hectares in the Intermountain West. Approximately 18.9 million ha of these woodlands occur within the range of sagegrouse and under current climatic conditions, and in the absence of fire, these woodlands will continue to expand (Betancourt 1987, West and Van Pelt 1986, West 1999a, Miller et al. 2000). Where juniper gains dominance in mountain big sagebrush communities, shrub cover declines to <1% (Miller et al. 2000) and the season of available succulent forbs is shortened because of rapid soil moisture depletion (Bates et al. 2000). On warmer, drier sites, high intensity crown fires may cause woodlands with depleted understories to transition to annual dominated communities (Tausch 1999; Fig. 3 and 4)

The second scenario, which has most extensively occurred in the Wyoming big sagebrush cover type, is the invasion of annual grasses. Invasion by exotic annuals has resulted in dramatic increases in both size and frequency of fire (Young and Evans 1973, Whisenant 1990, Swetnam et al. 1999, Tausch 1999, West 2000). For example, Whisenant (1990) reported MFRI in Wyoming big sagebrush communities has been reduced from 50–100 years to < 10 years. Repeat fires have allowed cheatgrass and other introduced annuals to replace the native shrub and herb layers. As early as the 1930s, range managers were aware of the rapid invasion of cheatgrass following fire (Stewart and Hull 1949). Cheatgrass now dominates or has a significant presence on 6.9 million ha of Great Basin rangeland (Pellant 1994), and over much of this area, annual-dominated communities can be considered a new steady state (Laycock 1991). These fine fuels shift fire seasonality to the more active growing period of native perennials (Whisenant 1990). The end results are that herbaceous cover varies greatly from year to year depending on moisture availability, shrub cover is absent, the season of available green plant material is shortened, high quality perennial forbs are scarce, and forage is absent in late summer through winter.

Risk of invasion by Mediterranean annuals in Wyoming and basin (*Artemisia tridentata* ssp. *tridentata* Nutt.) big sagebrush communities increases below elevations of 1500 m and becomes extreme below 1000 m. Exotic annual grasses such as cheatgrass will not usually dominate more mesic and cooler sagebrush types characterized by mountain big sagebrush and low sagebrush. Wyoming big sagebrush growing on old parent materials (low nutrient status, e.g., West and Yorks 2002) and colder sites, such as the high deserts in central Nevada, southern Utah, and southwestern Wyoming, also appear to be more resistant to cheatgrass invasion. Colder temperatures lower and delay ger-

026506

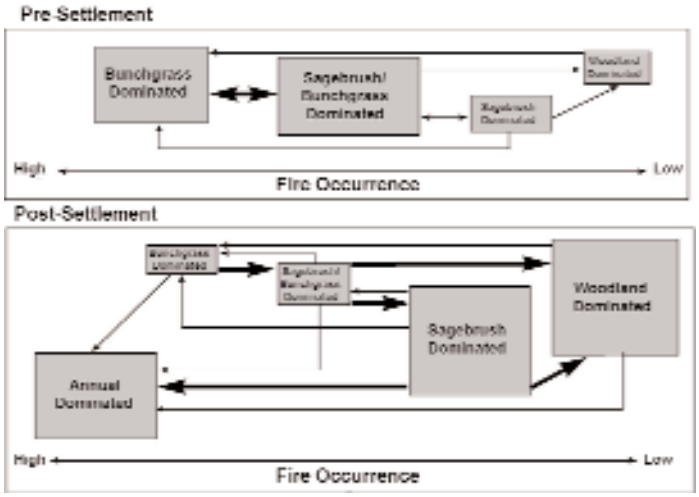


Fig. 3. Conceptual model illustrating pre and post-European settlement shrubland and woodland dynamics. Changes in box sizes represents shifts in area occupied by the different cover types. Heavy arrows indicate most common successional pathways. Adapted from Miller and Tausch 2001.

mination and slow down phenological development of cheatgrass. Competition from native herbaceous species may also be greater in these cooler and more mesic plant communities. Cheatgrass usually fares poorly in black sagebrush communities. Medusahead (*Taeniatherum asperum* Simonk.), however, can become abundant on some low sagebrush sites below 1500 m, especially where clay content is high (Dahl and Tisdale 1975, West and Young 2000).

Secondary weed species such as squarrose knapweed (*Centaurea squarrosa* Willd), rush skeleton weed (*Chondrilla juncea* L.), and bur buttercup (*Ranunculus testiculatus* Crantz) are rapidly invading cheatgrass and native plant communities in the Intermountain West, especially on ecological sites where Wyoming big sagebrush once dominated. Squarrose knapweed, like cheatgrass, produces an abundance of fine fuels. Continued spread of these secondary weeds shortens fire return intervals, increases the homogeneity and size of fires across the landscape, and threatens the integrity of Wyoming big sagebrush habitat.

Implications to sage-grouse and research needs

A limited number of studies have produced mixed reports on the impact of fire on sage-grouse populations (Rowland and Wisdom 2002). This is not entirely surprising given that the impact of fire on sage-grouse habitat is contingent on a large number of factors, including site potential, ecological condition, limiting functional plant groups, and the pattern, size, and season of burning. Additionally, most studies investigating the effects of fire on sage-grouse have been short-term (<10 years) (e.g., Bensen et al. 1991, Fischer et al. 1996). The lag response of sage-grouse combined with the long time periods typically needed by sagebrush to reestablish after fire, suggest that the ultimate evaluation of impacts of fire on sage-grouse habitat is to determine long-term use of burned and unburned areas, as well as periodic evaluation of plant community structural diversity over time, since burned areas will change in habitat suitability over time.

The impact of fire on the structure and composition of sage-grouse habitat may be positive or negative. Fire can enhance native perennial forbs and grasses, particularly where sagebrush is abundant, good populations of native herbs are present, and exotic species are limited. This most often applies to mountain big sagebrush communities where shrub canopy cover can exceed 35% and perennial forbs can increase 2 to 3 fold following fire (Blaisdell 1953, Miller unpublished data). However, the response of perennial forbs and grasses following fire can be highly variable (Harniss and Murray 1973, Nelle et al. 2000). Fire can lengthen the growing season for forbs important to sage-grouse (Wrobleski 1999), enhance the nutrient quality of forbs (McDowell 2000), and sage-grouse have been reported to be attracted to burned areas during the brood-rearing period (Klebenow and Beall 1977, Martin 1990). Limited research indicates

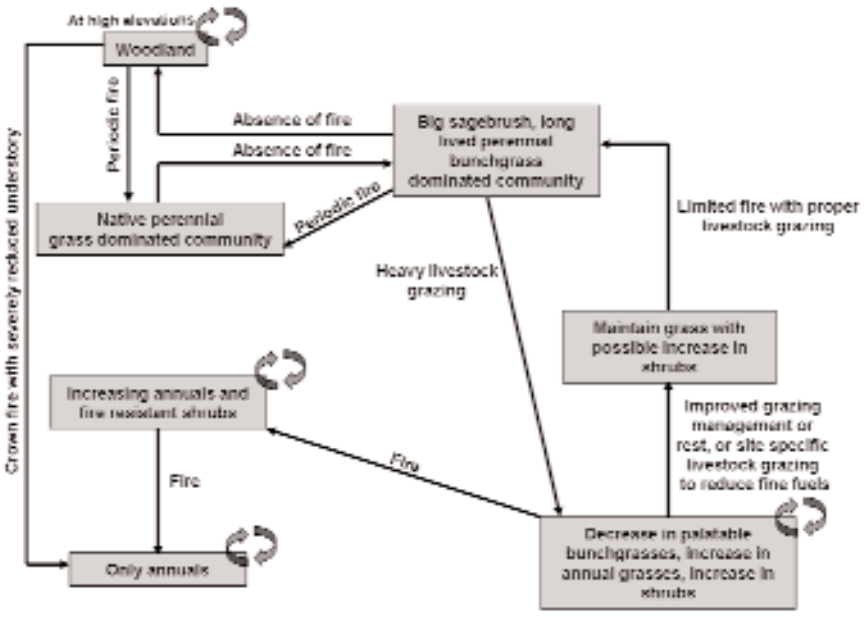


Fig. 4. Hypothesized relationship of grazing and fire to successional dynamics in sagebrush plant communities. Curved arrows indicate potentially steady states requiring management intervention to change community type to one more desirable for sage-grouse habitat. Movement to annual-dominated communities predominantly occurs in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Welsh) and at elevations below 1500 m, but can occur following crown fires in woodlands with severely depleted understories. The specific elevation for transitional thresholds to annual or woodland communities will vary regionally. Adapted from West 1989.

026507

that ants and beetles initially increase with fire in mountain big sagebrush communities but are not affected long-term (Nelle et al. 2000). Periodic fires with intervals less than 50 years will prevent negative habitat effects associated with pinyon and juniper encroachment into shrub steppe communities (Miller and Tausch 2001). In areas where grasses and shrubs have been drastically reduced or eliminated due to conifer dominance, mechanical pre-treatment of conifers can be used to promote fine fuel production. In addition, prescribed fires can break up fuel continuity, reducing the threat of future large and more complete burns.

Negative impacts of fire on sage-grouse habitat may include removal, at least temporarily, of the sagebrush overstory, thus decreasing the value of affected communities as winter and nesting habitat. In Wyoming big sagebrush dominated communities, there is little evidence that fire will enhance sage-grouse habitat where there is already a balance of native shrubs, perennial grasses, and forbs. Burning in these communities does not significantly increase desirable forbs used as sage-grouse food (Fischer et al. 1996, Miller unpublished data) and abundance of beetles (Hymenoptera), an important chick food (Pyle and Crawford 1996), may decrease (Fischer et al. 1996) or be unaffected (Pyle and Crawford 1996). Fire should not be used where sagebrush cover is the limiting factor for sage-grouse or where introduced annuals have replaced native perennial forbs and grasses. When deciding whether to burn on arid/low elevation sites, or in the Wyoming big sagebrush cover type, managers must balance the desired mix of plant communities with local assessments of the ability of shrubs to re-establish post-fire, and the potential for fire-induced annual grass dominance. In addition, some herbaceous species such as Idaho fescue (*Festuca idahoensis* Elmer) are sometimes decreased by fire and can require long time intervals for recovery (Wambolt et al. 2001). The amount of less palatable shrubs that resprout [rabbitbrush, horsebrush (*Tetradymia* spp. DC.), and broom snakeweed (*Gutierrezia sarothrae* Lag.)] should also be considered. These species typically increase following a burn but may be replaced by sagebrush in the absence of frequent disturbances (Young and Evans 1974). The impact of fire on the ecology of other *Artemisia* species, such as mid to high elevation silver sagebrush (*Artemisia cana* Pursh) communities, is not well understood.

The goal of managing sage-grouse habitats for an optimal balance of shrubs, forbs, and grasses at community and landscape scales should be analogous with restoring and or maintaining form, function, and process in sagebrush-dominated habitats. However, many questions remain regarding the impact of fire on sage-grouse habitat. For instance there is only limited documentation on the rate, variability, and environmental factors affecting sagebrush re-establishment in burns, and post-fire restoration of native herbaceous and shrub species in lower-elevation sagebrush communities has met with only limited success. The importance of successful restoration increases in proportion to the likelihood of post-fire annual grass invasion. The spatial and temporal effects of fire at landscape scales has received only limited attention, and should be addressed in concert with determining the landscape-scale mosaic of seral stages that provides optimal habitat for sage-grouse.

Livestock grazing

Livestock grazing has been extant in sagebrush plant communities for more than a century. However, only a few studies have directly addressed the effects of livestock grazing on habitat use by sage-grouse. Consequently, rangeland and wildlife managers must rely, with caution, on indirect evidence for guidance. Livestock grazing may affect sage-grouse habitat directly by altering structural habitat factors or plant community composition, or indirectly by altering abiotic processes (e.g., MFRI) and invasibility of sagebrush plant communities. While the impact of grazing on sagebrush plant communities varies with site potential, ecological condition, and climate variables, the aspects of livestock grazing that are controlled by management are, principally, the timing and intensity of defoliation.

Livestock grazing history

Herbivory as a disturbance of sagebrush-dominated plant communities existed prior to the arrival of domestic livestock in sage-grouse habitat (Burkhardt 1996). However, the proliferation of domestic livestock in the latter 1800s represented a fundamental change in the diversity of dominant herbivores, and the timing, and selection pressures associated with herbivory (Miller et al. 1994). Historic grazing practices centered around season-long use with stocking rates far exceeding carrying capacity (Young and Sparks 1985). The net impact of these grazing practices on sagebrush-dominated plant communities was an increase in shrub abundance, a decrease in perennial grasses, and the proliferation of non-native annual grasses (Young et al. 1972, 1976). By 1900, cattle and sheep on western rangelands totaled over 30 million animals (Wagner 1978). Cattle and sheep AUM's on federal land declined since the early 1900s (Council for Agricultural Science and Technology 1974, Laycock et al. 1996) and decreased more than 25% in the last 40 years (USDI-BLM 1990). Concurrent with reduced stocking of public rangelands has been measurable improvements in range condition during the latter half of the 1900s (Box 1990, Laycock et al. 1996).

Timing and intensity of livestock grazing

Research suggests that moderate livestock grazing or less in mid to late summer, fall, or winter is generally compatible with the maintenance of perennial grasses and forbs in sagebrush habitat (Pechanec and Stewart 1949, Mueggler 1950, Laycock and Conrad 1967, 1981, Gibbens and Fisser 1975, Miller et al. 1994, Bork et al. 1998). Herbaceous species in sagebrush plant communities are predominantly cool-season (C-3) plants that are vulnerable to defoliation during late spring and early summer. Heavy grazing (approximately 60% or greater utilization by weight) during this time has predictable results: 1) the vigor, yield, and cover of late-seral grasses and forbs decrease; 2) early-seral species (including annual grasses) may increase; 3) sagebrush density and canopy cover may increase (Craddock and Forsling 1938, Pechanec and Stewart 1949, Mueggler 1950, Laycock 1967, Bork et al. 1998); and 4) transition of sagebrush uplands to higher ecological status is inhibited (Mueggler 1950, Eckert and Spencer 1986, Laycock 1987; Fig 4.).

Moderate use has traditionally been defined as occurring within the range of 40–60% utilization by weight, however, generalizing a specific level of utilization that represents "proper use" can be difficult (Caldwell 1984). These difficulties arise in part due to lack of consistency in measurement technique (Frost et al. 1994), and the variable impact of a given level of utilization on plant communities in accordance with plant species present, site conditions, and climate variables. Some perennial grasses, such as Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker), needle-and-thread (*Stipa comata* Trin. & Rupr.), Nevada bluegrass (*Poa nevadensis* Vasey ex Scribn.), and Sandberg bluegrass, can withstand severe grazing (approximately 80% or greater utilization) as long as defoliation does not occur dur-

026508

ing the plants' reproductive period (Pearson 1964). Other grasses such as Idaho fescue, Thurber needlegrass (*Stipa thurberiana* Piper), and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith) decrease with heavy grazing (Rickard et al. 1975, Eckert and Spencer 1987). Restoration of sites in poor ecological condition may benefit from reduced utilization (Holechek et al. 1999) or rest (Fig. 4). Additionally, grazing tolerance of sagebrush-dominated plant communities can decrease with drought conditions and increase in periods of above average precipitation (Westoby et al. 1989). When used in conjunction with other information sources (e.g., weather data, non-livestock sources of herbivory) utilization data can be a valuable tool for helping to interpret the influence of livestock herbivory on vegetation trend (Sanders 1998). However, utilization data are not a substitute for long-term vegetation monitoring, and management objectives should be based on desirable vegetation composition over time, not utilization guidelines (Sharp et al. 1994, Burkhardt 1997, Sanders 1998).

Cattle, sheep, and horses (*Equus caballus*) in sagebrush habitat eat grass-dominated diets in all seasons of the year (Severson et al. 1968, Harrison and Thatcher 1970, Mackie 1970, Uresk and Rickard 1976, Olsen and Hansen 1977, Reiner and Urness 1982, Krysl et al. 1984, Ngugi et al. 1992, Crane et al. 1997, Glidewell et al. 2001) although sheep may consume a higher percentage of their diet as forbs. Livestock usually consume little to no sagebrush (< 10%) unless snow depth exceeds 20 cm (Harrison and Thatcher 1970), but winter sheep use of low elevation basin big sagebrush may be much greater (Cook et al. 1954). Sheep grazing in fall favors production of perennial forbs, whereas spring grazing can decrease forb production (Bork et al. 1998). Reduced sagebrush canopy cover in fall-grazed pastures (Mueggler 1950, Laycock 1967, Bork et al. 1998) is caused largely by competition from healthy grasses and forbs, rather than fall livestock browsing of sagebrush (Wright 1970).

Sagebrush cover generally increases as utilization of the herbaceous understory increases (Wright and Wright 1948, Pechanec and Stewart 1949, Mueggler 1950, Laycock 1967, Bork et al. 1998). But, once sagebrush cover reaches an upper threshold, livestock exclusion may have little effect on reversing the immediate trend (Johnson and Payne 1968, Rice and Westoby 1978, Sanders and Voth 1983, Wambolt and Payne 1986). Over long time intervals (40 years or more), sagebrush abundance may decline with a concomitant increase in understory herbaceous species (Anderson and Inouye 2001). On Wyoming big sagebrush sites with dense sagebrush and an understory of annual grasses, reductions in livestock grazing can hasten further habitat degradation if ungrazed fuel loads promulgate wildfires that burn uniformly and kill sagebrush on vast areas (Peters and Bunting 1994, West 1999b; Fig. 4).

Timing of grazing greatly influences the effects of livestock grazing in meadows and riparian areas. These sites are particularly vulnerable in late summer when excessive grazing and browsing may damage riparian shrubs, reduce the yield and availability of succulent herbs (Kovalchik and Elmore 1992), and cause deterioration of riparian function over time (Klebenow 1985). However, moderate utilization by livestock in spring, early summer, or winter is sustainable in non-degraded meadow and riparian areas within sagebrush habitat (Shaw 1992, Clary et al. 1996, Mosley et al. 1997). Moderate use equates to a 10-cm residual stubble height for most grasses and sedges and 5-cm for Kentucky bluegrass (Mosley et al. 1997, Clary and Leininger 2000). Shrub utilization should not exceed 50–60% during the growing season, and at least 50% protective ground cover (i.e., plant basal area + mulch + rocks + gravel) should remain after grazing (Mosley et al. 1997). While hydrophytic shrubs may not directly serve as sage-grouse habitat, they do impact the stability of riparian and meadow habitats important to sage-grouse (Winward 2000). The length of time livestock have access to meadows may be more important than the level of utilization; it has been suggested that livestock access be limited to < 3 weeks (Myers 1989, Mosley et al. 1997). In riparian and meadow habitat degraded by heavy livestock utilization, rest from grazing may be necessary for recovery (Clary and Webster 1989).

Implications to sage-grouse and research needs

It is probably safe to assume that historic grazing practices had strong negative impacts on sage-grouse habitat and perhaps populations (Patterson 1952, Wallestad 1975, Beck and Mitchell 2000), although definitive historical population data do not exist. However, research directly addressing the population-level impact of current livestock grazing practices on sage-grouse is lacking (Connelly et al. 2000). As noted previously, livestock AUM's have decreased and range condition has increased on federal lands since the mid 1900's, however, there has not been a concomitant increase in sage-grouse populations during the same time interval. This does not necessarily indicate a lack of association between grazing and sage-grouse populations, given that

1.) "improved" range condition (mainly increases in perennial bunchgrass abundance) associated with better livestock management practices may or may not equate to improvement in all habitat needs of sage-grouse,

2.) those plant communities displaying steady state dynamics may not change linearly with reduced stocking,

3.) it is unknown what portion of the areas with reduced stocking represent critical sage-grouse habitat, and

4.) the complicated nature of sage-grouse population dynamics may preclude their short-term response to management activities. Additionally, there has also been continued habitat loss through other factors (e.g., annual grass invasion, juniper encroachment, cultivation, road construction, powerline development, etc.).

A recent modeling exercise (Wisdom et al. 2002) incorporated 50 and 100% reductions in the detrimental effects of livestock grazing into a population level model for sage-grouse in the Interior Columbia Basin. The model predicted improved performance of sage-grouse populations with a combination of active habitat restoration and reduced livestock stocking rate, and equated reductions in livestock stocking rate to decreased detrimental effects of livestock on sage-grouse habitat at a 1 to 1 ratio. While this approach may appear empirically appealing in that it allows "what if" scenario modeling, caution is merited when assuming that reductions in livestock stocking rate are in a constant 1 to 1 ratio with changes in sage-grouse habitat quality, given that the exact slope of this relationship is unknown (it may be substantially greater or less than 1) and is variable in accordance with timing and intensity of livestock grazing, environmental factors, and specific type of sage-grouse habitat (e.g., nesting, brood-rearing, etc.). Given the complexity of the successional dynamics of sagebrush plant communities, combined with the multivariate nature of the effects of livestock grazing on these plant communities, it remains difficult to draw large-scale (time and space) conclusions regarding the impact of current livestock grazing practices on sage-grouse populations.

Livestock grazing may positively or negatively affect the structure and compo-

026509

sition of sage-grouse habitat. Brood-rearing habitat may be enhanced by grazing practices that favor upland forb production (e.g., fall grazing) and prescribed light (< 40%) to moderate spring grazing can remove standing herbage and make forbs more accessible (Smith et al. 1979, Fulgham et al. 1982). However, consumption of forbs by livestock may limit their availability to sage-grouse (Call 1979). In riparian brood-rearing habitat, sage-grouse prefer the lower vegetation (5–15 cm vs. 30–50 cm; Oakleaf 1971, Neel 1980, Klebenow 1982, Evans 1986) and succulent forb growth stimulated by moderate livestock grazing (Neel 1980, Evans 1986). Prescribed livestock grazing in spring and early summer, especially by sheep and goats (*Capra hircus*), can help control invasive weeds (Mosley 1996, Olson and Wallander 2001, Merritt et al. 2001) and woody plant encroachment (Riggs and Urness 1989) in sage-grouse habitat and may reduce wildfire risks to low elevation plant communities. However, the logistics of applying such grazing treatments at large spatial scales remain difficult.

Excessive livestock grazing has negatively impacted sage-grouse habitat by creating seral conditions that favor annual grass dominance and by reducing perennial grasses used as nesting and escape cover (Beck and Mitchell 2000). However, the specific relationship between grazing pressure and sage-grouse nest success has not been empirically evaluated. Heavy use of riparian meadows by livestock reduces the availability of succulent plant species and may induce avoidance of these habitats by sage-grouse (Neel 1980, Klebenow 1982, 1985). Nest destruction by livestock trampling is rare, however, the presence of livestock can cause sage-grouse to abandon their nests (Rasmussen and Griner 1938, Patterson 1952, Call 1979). Managers should consider delaying grazing of known nesting areas until after nesting (Beck and Mitchell 2000).

Rotational grazing systems are one way to provide areas (i.e., pastures) free from livestock disturbance during nesting. This benefit may be offset if heavy use occurs in the grazed pastures (Holechek et al. 1982), especially since sage-grouse can display high site fidelity (Fischer et al. 1993). One advantage of rest rotation grazing is that rested pastures can provide emergency forage (Ratliff and Reppert 1974), which may prevent excessive grazing in the used pastures during drought. This added residual cover may be important to sage-grouse, but light to moderate utilization of grasses in well-managed continuously grazed systems may also provide sufficient residual cover. Grazing systems in riparian areas have met with mixed results and their influence on system recovery and vegetation response will vary based on site potential, ecological condition, stream morphology, and climate (Elmore and Kauffman 1994). Compared with no grazing, rest rotation grazing increased forb abundance on sage-grouse meadow habitat in Nevada (Neel 1980).

Additional research is needed to address the direct effects of livestock grazing management on sage-grouse. Given the limited research base, much of what needs to be done is basic in nature. For example, research is needed to examine the effects of grazing variables such as timing, intensity, frequency, and stock density on sage-grouse habitat use patterns, nest success, and population dynamics. Additionally, research should continue to address the impacts of livestock grazing on patterns of plant succession at multiple space and time scales. This research should include both direct effects, as well as the interactive effects of grazing and abiotic factors (e.g., fire frequency) on plant succession.

Herbicide

Control of sagebrush has impacted large portions of rangeland in the western U.S. By the 1970's, over 2 million ha of sagebrush had been mechanically treated, sprayed, or burned (Schneegas 1967, Vale 1974). This practice has been widely associated with declines in sage-grouse habitat quality (Connelly et al. 2000). Much of the research literature has focused on maximum sagebrush kill in strips or blocks, but recent work has examined the impact of selective thinning of sagebrush on wildlife habitat quality (Baxter 1998).

Where sagebrush density is high enough to limit understory expression of forbs and grasses, some reduction of sagebrush may be desirable (Laycock 1991). Initial efforts to control sagebrush used 2,4-D [(2,4-dichlorophenoxy) acetic acid], which was effective in suppressing big sagebrush and typically resulted in dramatic increases in herbage production (Orpet and Fisser 1979, Waltenberger et al. 1979, Kearl and Freeburn 1980). The impact of 2,4-D on forb abundance varies by species (Table 3). Concerns over reduced plant diversity following 2,4-D have severely limited its use. Tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea), a photosynthesis inhibitor with soil activity greater than 1 year, was introduced in 1973 and can selectively control big sagebrush at low application rates. Recent studies have demonstrated that big sagebrush canopy cover is reduced in proportion to application rate, with simultaneous progressive increases in understory grass and forb abundance (Whitson and Alley 1984, Whitson et al. 1988, Halstvedt 1994, Olson et al. 1994, 1996, Johnson et al. 1996, Olson and Whitson 1996, 2002). For example, Halstvedt et al. (1996) reported a 59–491% increase in native perennial grass production following reduction of pre-treatment big sagebrush canopy cover (25–35%) to 12–15% after 10–17 years following tebuthiuron thinning treatments. Forb production increased between 15–127% on treated sites. Herbicides offer some advantages to mechanical manipulation of sagebrush including cost effectiveness, longer treatment life, less damage to non-target shrub species, decreased erosion risk, and better control of the extent of sagebrush kill (Blaisdell et al. 1982, Olson et al. 1994, Baxter 1998).

Implications to sage-grouse and research needs

Block or strip applications of herbicide at rates that severely diminish sagebrush will likely have negative impacts on sage-grouse habitat quality. In lekking habitat, some researchers report decreases in sage-grouse males following sagebrush removal (Wallestad 1975, Connelly et al. 1981), while others have found no clear effect (Gates 1985, Martin 1970, Benson et al. 1991, Fischer 1994). Sage grouse may cease to use block treated areas as nesting habitat (Klebenow 1970) and winter habitat degradation is proportional to severity of sagebrush kill (Connelly et al. 2000). Increases in forb availability in strip or block-sprayed habitat may increase the value of these areas as brood-rearing habitat (e.g., Autenrieth 1969) but use patterns often indicate avoidance of treated areas (Klebenow 1970, Braun et al. 1977).

It has been suggested that thinning treatments can be used as a tool to manage sage-grouse habitat (Beck and Mitchell 2000). Lekking habitat is rarely limited, but in areas where dense, monotypic big sagebrush stands limit suitable lekking grounds, sagebrush thinning can create small open areas for breeding activities. Sage-grouse have been reported to use newly disturbed sites as leks (Connelly et al. 1981). In localized areas, reduced application rates of tebuthiuron can be used to thin big sagebrush cover and

026510

increase understory perennial grasses and forbs associated with nesting and brood-rearing habitat. Thinned Wyoming big sagebrush stands may have maximum forb production at 11 to 17% sagebrush canopy cover (Johnson et al. 1996). Where sage-grouse winter cover is limited, thinning of big sagebrush should be avoided (Klebenow 1985, Robertson 1991). Connelly et al. (2000) recommended that treatments be limited to < 20% of the breeding habitat (depending on sagebrush type) within a 20 to 30-year period, primarily because of concerns over damage to winter habitat. Additional research is needed to further identify the impact of sagebrush thinning on habitat use by sage-grouse.

Herbicides can also be used to control invasive annual plant species in sage-grouse habitat. For instance, herbicides may be useful in controlling cheatgrass abundance (Mosley et al. 1999, Pellant et al. 1999). Herbicides such as imazapic (Plateau) applied prior to cheatgrass emergence can be used to release forbs and perennial grasses in the understory (Whitson 2003). Herbicide control of cheatgrass has positive implications to the maintenance of communities in danger of transitioning to annual-dominated states, and, when used in conjunction with native grass seeding, the restoration of sites that have already realized that transition. This latter practice has been suggested as a form of active restoration of sage-grouse habitat degraded by annual grass dominance (Hemstrom et al. 2002).

Landscape issues in sage-grouse management and research

The foregoing outlines, 1) the relatively complex life cycle of sage-grouse; 2) the collective observations of the bird in the many different kinds of habitat it requires throughout the year; and 3) different ways that individual birds and populations can be affected by abiotic, biotic, and management factors. It is important to realize that this information has been accumulated piecemeal (i.e., by many different people working in different places and at different times). Thus, compositing this information to form our understanding and creating guidelines for management (e.g., Connelly et al. 2000) is based largely on data taken from small areas over short times. This process may give a deceptive picture, both generally and specifically, for any given population. For instance, there may be differing causes of mortality in different places, at different times, particularly between migratory and resident populations. Some of the studies could involve shrinking populations, whereas others could involve stable to growing populations. The type of population present in each study needs to be identified because they require different types of management responses.

It is now apparent that rather than one, a few to many causes may be synergistically and cumulatively operating to diminish sage-grouse. For instance, reducing predator control may occur simultaneously with undesirable changes in vegetation structure triggered by other factors (e.g., livestock grazing practices, fire control). While many believe that cause and effect mechanisms need to be disentangled for declining sage-grouse populations, others judge that to be neither feasible nor timely. Shrader-Frechette and McCoy (1993) emphasize that solving complex issues, like sustaining sage-grouse populations, will be more tractable in a case study mode.

Linking habitat and population changes

Researchers and managers have long had a vague, qualitative notion that sage-grouse respond to negative changes within entire landscapes (Connelly et al. 2000), portions of which the birds use at various times of the year. Until recently, however, a ready means of quantifying landscape patterns and change was lacking. Now, geomatics [combined remote sensing (RS), global positioning systems (GPS), and geographic information systems (GIS)], can be employed to give quantitative expressions and visualizations of habitat patterns over large areas of land for the past several decades. Landscape ecology (Turner et al. 2001) provides a logical framework and a new set of tools to examine how spatial arrangements of different kinds of habitat may influence individuals and populations. Intermediate-sized landscapes of 250,000 to 2.5 million ha and their macro-mosaics of ecological sites and stands in various seral stages seem to be the most appropriate scale for management solutions to be successful, since improvements in only part of the year-round habitat may be negated by degradation in other nearby habitat needed at other times. Successful management at the scale of the entire geographical range of the species is unlikely because all races of sage-grouse may not have the same habitat requirements or respond to environmental changes and management in identical ways.

By combining landscape ecology and geomatics, it is now possible to characterize both current spatial patterns and changes in these geographic patterns over about the past 50 years by analyzing archived imagery. Data coverage of entire landscapes in the range of 100,000 to 250,000 ha is now feasible, as illustrated in the recent work of Washington-Allen (2003) at the Deseret Ranch in northeastern Utah. Patches of land can be characterized as to cover dominance by plant growth forms and bare ground. Fragmentation and coalescence, patch sizes and boundary shapes and proximity to similar and dissimilar patches can be tracked over time. Underlying GIS layers dealing with management and disturbance history, along with soils, ecological site [as provided by Natural Resource Conservation Agency (NRCS) databases] and seral status can be connected to indicators of sage-grouse abundance. A similar approach at large scales (1km^2 pixels) was recently used to characterize habitat changes in the Interior Columbia Basin (Hemstrom et al. 2002).

Sage-grouse is not a species that can thrive only where large homogeneous stands of any single plant species occupy the bulk of the landscape. While recommendations exist for the kinds of habitats that are preferred at different times in the life cycle of the bird (Connelly et al. 2000), the proportions of habitats that are optimum or even tolerable remains unknown. It is likely that sage-grouse are responding to habitat attributes at multiple scales while other sagebrush obligates may be responding at different scales. These questions can now be addressed by applying concepts from landscape ecology linked through geomatics technology. This will allow natural resource professionals to break away from their traditions of collecting only short runs of point-based data focused on either livestock or wildlife species and the plant communities in which they are found.

We suggest that areas where sage-grouse have recently diminished be collectively identified. From archived aerial photos and satellite imagery, fundamental changes in the landscape can be quantified via time series of landscape metrics (Turner et al. 2001) and other RS/GIS based indicators (Washington-Allen 2003). Another useful effort would be to characterize and compare the landscapes holding non-migratory populations to those that are migratory. The existence of non-migratory populations implies that all habitat requirements of sage-grouse are sometimes met in one relatively small area. In these areas, the mix of habitats

026511

and their proportions needs to be defined. Similar studies involving lesser prairie chickens (*Tympanuchus pallidicinctus*) have suggested some factors that land managers can pro-actively address (Woodward and Fuhlendorf 2001).

The approach suggested above will require a level of collaboration rarely seen between landscape ecologists and wildlife and range scientists. Many different landowners and managers will need to be involved because landscapes frequently cross ownership and political boundaries. Non-governmental organizations such as the North American Grouse Partnership could serve to facilitate such activities crossing jurisdictional boundaries. The Western Association of Fish and Wildlife Agencies should also foster such work, promoting cooperation between states and ecologists and managers with broad expertise.

Another aspect that needs to be addressed frontally is the choice of how and what to study. If the details of quantification of various aspects of environment and biota (e.g., sagebrush cover, Miller et al. 2003) are not agreed upon from the outset, time and trust will be dissipated during the inevitable arguments about interpretation of results. Because the sage-grouse issue is of regional concern, it needs to be approached in a multi-state fashion. If different states and other jurisdictions take differing approaches, arguments about the confoundments of place, times, and methods might persist interminably.

Some Final Thoughts

Management of sage-grouse populations and their habitat is set within the political and sociologic tendency to focus on individual pieces of the overall management challenges. However, the ecology and management history of sage-grouse and their habitat combine to suggest a more complex, multivariate relationship, and to focus on any single issue (e.g., livestock grazing, fire regime, other land management practices, disease, predation) is to deny the complexity of the overall situation. The take home message is that solutions will involve a diversity of management and research professionals working in concert to solve multifaceted problems.

In a broader spatial and temporal context, the sage-grouse decline may be symptomatic of long-term regional level problems. While sage-grouse are currently at the center of ecological and political concern, other species, mainly sagebrush obligates [e.g., Brewer's sparrow (*Spizella pallida)*, pygmy rabbit (*Brachylagus idahoensis*), sagebrush vole (*Lagurus curtatus*)], are also declining, suggesting that "fixing" the sage-grouse problem should be synonymous with improvements at the ecosystem level. This point may be of particular importance given the burgeoning number of local and state-level sage-grouse working groups in the western US. If system level problems are not addressed now, the efforts of these working groups will have to be repeated for other sagebrush obligates, as additional species take political front and center over time. Regional level dialogue and planning should be facilitated by the Interagency Sage Grouse Conservation Framework Team, which provides an effective linkage between state level conservation efforts. Access to the data needed to make large-scale decisions has been aided by the SAGEMAP project (http://sagemap.wr.usgs.gov), which serves as a storehouse for spatial data pertaining to conservation of sage-grouse and sagebrush-dominated plant communities.

Natural resource professionals of all walks should strive to keep an open mind regarding the potential structure of plant communities serving as sage-grouse habitat. A good example is the amount of sagebrush cover a given community can be expected to produce. It is quite probable that differences of opinion on this matter are due to differences in vegetation sampling methodology. In such cases, published ecological site information can be a useful intermediary for helping find common ground (e.g., NRCS data, Tisdale et al. 1965, Winward 1970, Mueggler and Stewart 1980). Natural resources professionals should also consider that without purposeful habitat management (e.g., prescribed fire-based juniper control) successional changes may decrease the value of some plant communities as sage-grouse habitat. Active management will likely be required to address the problem of annual grass invasion in sage-grouse habitat; a dilemma for which there is not currently a definitive solution over large scales.

Bringing together groups of professionals (e.g., range and wildlife specialists) in an effective manner involves coordinated planning. One potential avenue of cooperation would involve re-visiting past sage-grouse research efforts. If the precise geographic locations of these projects could be obtained, rangeland scientists could work in concert with wildlife scientists to identify big sagebrush subspecies and serally interpret the vegetation structure preferred by sage-grouse. This information could then be used as the basis of a succession-based model for predicting management impacts, and planning habitat manipulations. Such efforts must have active participation from both management and research entities; without management buy-in, significant amounts of time and energy can be wasted developing models that will never be used. As was previously pointed out, this is not a process that will produce quick results. Instead, time is needed for management actions to produce changes in habitat and other environmental variables before the impacts on sage-grouse populations can be manifested. Thus, it is imperative that such efforts be initiated as soon as possible.

Literature Cited

Aldridge, C.L. 2000. Reproduction and habitat use by sage grouse (*Centrocercus urophasianus*) in a northern fringe population. M.S. Thesis, Univ. of Regina, Regina, Saskatchewan.

Aldridge, C.A. and RM. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. J. Wildl. Manage. 66:433–444.

Anderson, J.E. and RS. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol. Monogr. 71:531–556.

Andrén, H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecol. 69:544B547.

Angelstam, P. 1986. Population dynamics in tetraonids: the role of extrinsic factors. Proc. of the Int. Ornithological Cong. 19:2458B2477.

Autenrieth, R.E. 1969. Impact of strip spray on vegetation and sage grouse use on summer habitat. Proc. of the Western States Sage Grouse Workshop 6:147–157.

Autenrieth, R.E. 1981. Sage grouse management in Idaho. Ida. Dept. Fish & Game.Wildl. Bull. 9. Boise, Ida.

Barnett, J.K. 1992. Diet and nutrition of female sage grouse during the pre-laying period. M.S. Thesis, Ore. St. Univ. Corvallis, Ore.

Barnett, J.K. and J.A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. J. Range Manage. 47:114–118.

Bates, J.D., R.F. Miller, and T. Svejcar. 2000. Understory vegetation response and nitrogen cycling following cutting of western juniper. J. Range Manage. 53:119–126.

Batterson, W.M. and W.B. Morse. 1948. Oregon sage grouse. Oregon Game Comm.Oregon Fauna Serv. 1. Portland, Ore.

Baxter, G. 1998. Thinning dense sagebrush stands with Spike 20P. Rangelands 20:14–16.

Bean, R.W. 1941. Life history studies of the Sage Grouse (*Centrocercus urophasianus*) in Clark County, Idaho. B.S. Thesis, Ut. St. Agr. Coll. Logan, Ut.

Beck, T.D.I. and C.B. Braun. 1978. Weights of Colorado sage grouse. Condor 80:241–243.

Beck, J.L. and D.L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildl. Soc. Bull. 28:993–1002.

026512

Benson, L. A., C. E. Braun, and W. C. Leininger. 1991. Sage grouse response to burning in the big sagebrush type. Proc. of Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Instit. 5:97–104.

Betancourt, J.L. 1987. Paleoecology of pinyon-juniper woodlands: summary, p. 129–139. *In:* R.L. Everett (ed.) Proceedings: Pinyon-juniper conference. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-215.

Blaisdell, J.P. 1953. Ecological effects on planned burning of sagebrush-grass range on the upper Snake River Plains. U.S.D.A. Tech. Bull. 1075. Washington, D.C.

Blaisdell, J.P., R.B. Murray, and E.D. McArthur. 1982. Managing inter-mountain rangelands-sagebrush-grass ranges. U.S.D.A., For. Serv., Gen. Tech. Rept. INT-134.

Blake, C.S. 1970. The response of sage grouse populations to precipitation trends & habitat quality in south central Idaho. Proc. West. Assoc. State Game and Fish Commissioners. 50:452-462.

Bork, E.W., N.E. West, and J.W. Walker. 1998. Cover components on long-term seasonal sheep grazing treatments in three-tip sagebrush steppe. J. Range Manage. 51:293-300.

Box, T.W. 1990. Rangelands, p. 101-120. *In:* R.N. Sampson, and W. Hair (eds.) Natural Resources for the 21st Century. Island Press, Wash. D.C.

Bradley, A.F., N.V. Noste, and W.C. Fischer. 1992. Fire ecology of forests and woodlands in Utah. U.S.D.A., For. Serv., Gen. Tech. Rept. INT-287.

Braun, C.E. 1998. Sage grouse declines in western North America: what are the problems? Proc. of the West. Assoc. of St. Fish and Wildl. Agencies 78:139-156.

Braun, C. E., T. Britt, and R.O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. Wildl. Soc. Bull. 5:99-106.

Browers, H.W. and L.D. Flake. 1985. Breakup and sibling dispersal of two sage grouse broods. Prairie Nat. 17:248-249.

Brown, D.E. and R. Davis. 1995. One hundred years of vicissitude: terrestrial bird and mammal distribution changes in the American Southwest, 1890-1990, p.231-244. *In:* L. F. DeBano, G. J. Gottfried, R. H. Hamre, C. B. Edminster, P. F. Ffolliott, and A. Ortega-Rubio (tech. coordinators) Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. U.S.D.A. For. Serv., Gen Tech Rept. RM-GTR-264.

Burkhardt, J.W. 1996. Herbivory in the Intermountain West. Univ. of Ida. For., Wildl. and Range Exp. Sta. Bull. 58.

Burkhardt, J.W. 1997. Grazing utilization limits: An ineffective management tool. Rangelands 19:8-9.

Burkhardt, J.W. and E.W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecol. 76:472–484.

Caldwell, M.M. 1984. Plant requirements for prudent grazing, p. 117-152. *In:* Nat. Res. Council/Nat. Acad. Sci. "Development Strategies for Rangeland Management." Westview Press, Boulder, Colo.

Call, M.W. 1979. Habitat requirements and management recommendations for sage grouse. USDI-BLM Denver Serv. Center Tech. Note 330.

Call, M.W. and C. Maser. 1985. Wildlife habitats in managed rangelands: The Great Basin of southeastern Oregon: sage grouse. U.S.D.A. For. Serv., Gen. Tech. Rept. PNW-187.

Clary, W.P. and W.C. Leininger. 2000. Stubble height as a tool for management of riparian areas. J. Range Manage. 53:562–573.

Clary, W.P. and B.F. Webster. 1989. Managing grazing of riparian areas in the Intermountain Region. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-263.

Clary, W.P., N.L. Shaw, J.G. Dudley, V. A. Saab, J.W. Kinney, and L.C. Smithman. 1996. Response of a depleted sagebrush steppe riparian system to grazing control and woody plantings. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-RP-492.

Connelly, J.W. and C.E. Braun. 1997. Long-term changes in sage grouse (*Centrocercus urophasianus)* populations in western North America. Wildl. Biol. 3:229-234.

Connelly, J.W., W.J. Arthur, and O.D. Markham. 1981. Sage grouse leks on recently disturbed sites. J. Range Manage. 34:153-154.

Connelly, J.W., H.W. Browers, and R.J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. J. Wildl. Manage. 52:116-122.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. Wildl. Soc. Bull. 28:967–985.

Connelly, J.W., W.L. Wakkinen, A.P. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. J. Wildl. Manage. 55:521–524.

Connelly, J.W., R.A. Fischer, A.D. Apa, K. P. Reese, and W.L. Wakkinen. 1993. Renesting by sage grouse in southeastern Idaho. Condor 95:1041–1043.

Connelly, J.W., K.P. Reese, W.L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Study I: Sage grouse response to a controlled burn. Ida. Dept. Fish & Game. Boise, Ida.

Conrad, C.E. and C.E. Poulton. 1966. Effects of wildfire on Idaho fescue and bluebunch wheatgrass. J. Range Manage. 19:138–141.

Cook, C.W., L.A. Stoddart, and L.E. Harris. 1954. The nutritive value of winter range plants in the Great Basin. Utah Agr. Exp. Sta. Bull. 372.

Council for Agricultural Science and Technology. 1974. Livestock grazing on federal lands in the 11 western states. J. Range Manage. 27:174–181.

Craddock, G.W. and C.L. Forsling. 1938. The influence of climate and grazing on spring-fall sheep range in southern Idaho. U.S.D.A. Tech. Bull. 600.

Crane, K. K., M. A. Smith, and D. Reynolds. 1997. Habitat selection patterns of feral horses in southcentral Wyoming. J. Range Manage. 50:374-380.

Crawford, J.A. and R.S. Lutz. 1985. Sage Grouse population trends in Oregon, 1941-1983. Murrelet 66:69-74.

Crawford, J.A., M.A. Gregg, M.S. Drut, and A.K. DeLong 1992. Habitat use by female sage grouse during the breeding season in Oregon. Final Report submitted to Bur. Land Manage., Ore. St. Univ. Corvallis, Ore.

Dahl, B.F. and E.W. Tisdale. 1975. Environmental factors related to medusahead distribution. J. Range Manage. 28:463-468.

Dalke, P.D., D.B. Pyrah, D.C. Stanton, J.E. Crawford, and E.F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. J. Wildl. Manage. 27:811–841.

Danvir, R.E. 2002. Sage Grouse ecology and management in a northern Utah sagebrush-steppe. Wildlife Research Report, Deseret Land and Livestock Inc. Woodroff, Ut.

Dargen L.M., R.J. Keller, H.R. Shepard, and R.N. Randall. 1942. Survey of 1941-42: food studies, parasite relations, habitat requirements, including preliminary data on sharp-tailed grouse in Moffat and Routt counties. Colo. Game and Fish Comm, Sage-grouse Survey 4. Denver, Colo.

DeLong, A.K. 1994. Relationships between vegetation structure and predation rates of artificial sage grouse nests. M.S. Thesis, Ore. St. Univ. Corvallis, Ore.

DeLong, A.K., J.A. Crawford, and D.C. DeLong, Jr. 1995. Relationships between vegetational structure and predation of artificial Sage grouse nests. J. Wildl. Manage. 59:88-92.

Drut, M.S., J.A. Crawford, and M.A. Gregg. 1994a. Brood habitat use by sage grouse in Oregon. Great Basin Natural. 54:170–176.

Drut, M.S., W.H. Pyle, and J.A . Crawford. 1994b. Technical note: Diets and food selection of sage grouse chicks in Oregon. J. Range Manage. 47:90–93.

Dunn, P.O. and C.E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621–627.

Dunn, P.O. and C.E. Braun. 1986. Late summer-spring movements of juvenile sage grouse. Wilson Bull. 98:83–92.

Eckert, R.E., Jr. and J.S. Spencer. 1986. Vegetation response on allotments grazed under rest-rotation management. J. Range Manage. 39:166–174.

Eckert, R.E., Jr. and J.S. Spencer. 1987. Growth and reproduction of grasses heavily grazed under rest-rotation management. J. Range Manage. 40:156–159.

Edelmann, F.B., M.J. Ulliman, M.J. Wisdom, K.P. Reese, and J.W. Connelly. 1998. Assessing habitat quality using population fitness parameters: a remote sensing/GIS-Based habitat-explicit population model for sage grouse (*Centrocercus urophasianus*). Ida. For., Wildl. & Range Exp. Sta. and Univ. Ida. Contribution 846. Moscow, Ida.

026513

Elmore, W. and B. Kauffman. 1994. Riparian and Watershed systems: Degradation and Restoration, p. 212–231. *In:* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.) Ecological Implications of Livestock Herbivory in the West. Society for Range Manage. Denver, Colo.

Emmons, S.R. and C.E. Braun. 1984. Lek attendance of male sage grouse. J. Wildl. Manage. 48:1023–1028.

Eng, R.L., E.J. Pitcher, S.J. Scott, and R.J. Greene. 1979. Minimizing the effects of surface coal mining on a sage grouse population by a directed shift of breeding activities, p. 464–468. *In:* G.A. Swanson (tech-co-ord) The mitigation symposium. U.S.D.A. For. Serv., Gen Tech. Rept. RM-65.

Evans, C. 1986. The relationship of cattle grazing to sage grouse use of meadow habitat on the Sheldon National Wildlife Refuge. M.S. Thesis, Univ. Nev., Reno, Nev.

Fischer, R.A. 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. M.S. Thesis Univ. Ida. Moscow, Ida.

Fischer, R.A., K.P. Reese, and J.W. Connelly. 1996. An investigation on fire effects within xeric sage grouse brood habitat. J. Range Manage. 49:194–198.

Fischer, R.A., W.L. Wakkinen, K.P. Reese, and J.W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038–1041.

Frost, W.E., E.L. Smith, and P.R. Ogden. 1994. Utilization guidelines. Rangelands 16:256–259.

Fulgham, K.O., M.A. Smith, and J.C. Malechek. 1982. A compatible grazing relationship can exist between domestic sheep and mule deer, p. 458–478. *In*: J.M. Peek and P.D. Dalke (eds.) Proc. of the Wildlife-Livestock Relationships Symp. Idaho For., Wildl. and Range Exp. Sta., Univ. Idaho, Moscow, Ida.

Gates, R.J. 1985. Observations of the formation of a sage grouse lek. Wilson Bull. 97:219–221.

Gibbens, R.P. and H.G. Fisser. 1975. Influence of grazing management systems on vegetation in the Red Desert region of Wyoming. Univ. of Wyo. Agr. Exp. Sta. Sci. Monogr. 29.

Gibson, R.M. and J.W. Bradbury. 1986. Male and female mating strategies on sage grouse leks, p. 379–398. *In:* D. I. Rubenstein and R. W. Wrangham (eds.) Ecological aspects of social evolution: birds and mammals. Princeton Univ. Press, Princeton, N.J..

Gill, R.B. 1966. Weather and sage grouse productivity. Colo. Game, Fish and Parks Dep., Outdoor Info. Leaflet 37. Denver, Colo.

Glidewell, B.C., J.C. Mosley, and J.W. Walker. 2001. Sheep and cattle response when grazed together on sagebrush-grass rangeland. Proc. West. Sec. Amer. Soc. Anim. Sci. 52:156–159.

Gregg, M.A. 1992. Habitat use and selection of nesting habitat by sage grouse in Oregon. M.S. Thesis, Ore. St. Univ. Corvallis, Ore.

Gregg, M.A., J.A. Crawford, and M.S. Drut. 1993. Summer habitat use and selection by female sage grouse (*Centrocercus urophasianus*) in Oregon. Great Basin Nat. 53:293–298.

Gregg, M.A., J.A. Crawford, M.S. Drut, and A.K. DeLong. 1994. Vegetative cover and predation of sage grouse nests in Oregon. J. Wildl. Manage. 58:162–166.

Gruell, G.E. 1999. Historical and modern roles of fire in pinyon-juniper, p. 24–28. *In:* S. B. Monsen and R. Stevens (eds.) Proc. Ecology and management of pinyon-juniper communities within the interior West.; Sept. 15–18, 1997, Provo, Ut. U.S.D.A. For. Serv. RMRS-P-9.

Halstvedt, M.B. 1994. Big sagebrush (*Artemisia tridentata*) management with reduced rates of tebuthiuron, p. 10-13. *In:* Big Sagebrush (*Artemisia tridentata*) Management With Spike 20P Herbicide (tebuthiuron). DowElanco, Indianapolis, Ind.

Halstvedt, M.B., V.F. Carrithers, T.D. Whitson, and G. Baxter. 1996. Thinning big sagebrush canopy cover using low rates of Spike 20P herbicide. Down To Earth 51:1–6.

Hamerstrom, F. N., Jr., O. E. Mattson, and F. Hamerstrom. 1957. A guide to prairie chicken management. Wis. Cons. Dept. Tech. Wildl. Bull. No. 15.

Hanf, J.M., P.A. Schmidt, and E.B. Groshend. 1994. Sage grouse in the high desert of Central Oregon: results of a study, 1988-1993. U.S.D.I.-Bur. Land Manage., Series P-SG-01, Prineville, Ore.

Harniss, R.O. and R.B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. J. Range Manage. 26:322–325.

Harrison, B.J. and A.P. Thatcher. 1970. Winter sheep grazing and forage preference in southwestern Wyoming. J. Range Manage. 23:109–111.

Hemstrom, M.A., M.J. Wisdom, W.J. Hann, M.M. Rowland, B. C. Wales, and R.A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the Interior Columbia Basin, U.S.A. Cons. Biol. 16:1243–1255.

Holechek, J.L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: What we've learned. Rangelands 21: 12–16.

Holechek, J.L., R. Valdez, S.D. Schemnitz, R.D. Pieper, and C.A. Davis. 1982. Manipulation of grazing to improve or maintain wildlife habitat. Wild. Soc. Bull. 10:204–210.

Houston, D.B. 1973. Wildfires in northern Yellowstone National Park. Ecol. 54:1109–1117.

Hulet, B.V., J.T. Flinders, J.S. Green, and R. B. Murray. 1986. Seasonal movements and habitat selection of sage grouse in southern Idaho, p. 168–175. *In:* E.D. McArthur, and G.L. Welch (compilers) Proc. a Symposium on the biology of *Artemisia* and *Crysothamnus*. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-200.

Hupp, J.W. and C.E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. J. Wildl. Manage. 53:823–829.

Ihli, M., P. Sherbenou, and C.W. Welch. 1973. Wintering sage grouse in the Upper Big Lost River. Idaho Acad. Sci. 1973:73–80.

Jenni, D.A. and J.E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring censuses. J. Wildl. Manage. 42:46–52.

Johnson, J.R. and G.F. Payne. 1968. Sagebrush reinvasion as affected by some environmental influences. J. Range Manage. 21:209–213.

Johnson, K.H., R.A. Olson, and T.D. Whitson. 1996. Composition and diversity of plant and small mammal communities in tebuthiuron-treated big sagebrush (*Artemisia tridentata*). Weed Tech. 10:404–416.

June, J.W. 1963. Wyoming sage grouse population measurement. Proc. West. Assoc. State Game and Fish Comm. 43:206–211.

Kearl, G.W. and J.W. Freeburn. 1980. Economics of big sagebrush control for mitigating reductions of federal permits. M.S. Thesis, Univ. Wyo. Laramie, Wyo.

Keller, R. J., H.R. Shepherd, and R.N. Randall. 1941. Survey of 1941: North Park, Jackson County, Moffat County, including comparative data of previous season. Colo. Game and Fish Comm. Sage Grouse Surv. 3. Denver, Colo.

Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. J. Wildl. Manage. 33:649–662.

Klebenow, D. A. 1970. Sage grouse versus sagebrush control in Idaho. J. Range Manage. 23:396–400.

Klebenow, D. A. 1982. Livestock grazing interactions with sage grouse, p. 113–123. *In*: J.M. Peek and P.D. Dalke (eds.) Proc. of the Wildlife-Livestock Relationships Symposium. Idaho For., Wildl., and Range Exp. Sta., Univ. Idaho. Moscow, Ida.

Klebenow, D. A. 1985. Habitat management for sage-grouse in Nevada. World Pheasant Assoc. 10:34–46.

Klebenow, D. A. and R. C. Beall. 1977. Fire impacts on birds and mammals on Great Basin rangelands, p. 1–13. *In:* Anonymous, Proc. Joint Intermountain Rocky Mountain Fire Research Council, Casper, Wyo.

Klebenow, D. A. and G. M. Gray. 1968. The food habits of juvenile sage grouse. J. Range Manage. 21:80–83.

Kovalchick, B. L. and W. Elmore. 1992. Effects of cattle grazing systems on willow-dominated plant associations in central Oregon, p. 111–119. *In*: W.P. Clary, E.D. McArthur, D. Bedunah, and C.L. Wambolt, (eds.) Proc. Symposium on Ecology and Management of Riparian Shrub Communities, U.S.D.A. For. Serv., Gen. Tech. Rept. INT-GTR-289.

Krysl, L. J., M. E. Hubbert, B. F. Sowell, G. E. Plumb, T. K. Jewett, M. A. Smith, and J. W. Waggoner. 1984. Horses and cattle grazing in the Wyoming Red Desert, I. Food habits and dietary overlap. J. Range Manage. 37:72–76.

Laycock, W. A. 1967. How heavy grazing and protection affect sagebrush-grass ranges. J. Range Manage. 20:206.

026514

Laycock, W. A. 1987. Grazing management systems and tactics in the sagebrush ecosystem, p. 40–48. *In*: J.A. Onsager, (ed.) Integrated Pest Management on Rangeland: State of the Art in the Sagebrush Ecosystem. U.S.D.A.-A.R.S. Bull. ARS-50.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. J. Range Mange. 44:427–433.

Laycock, W.A. and P.W. Conrad. 1967. Effect of grazing on soil compaction as measured by bulk density on a high elevation cattle range. J. Range Manage. 20:136–140.

Laycock, W.A. and P.W. Conrad. 1981. Responses of vegetation and cattle to various systems of grazing on seeded and native mountain rangelands in eastern Utah. J. Range Manage. 34:52–58.

Laycock, W.A., D. Loper, F.W. Obermiller, L. Smith, S.R. Swanson, P.J. Urness, and M. Vavra. 1996. Grazing on public lands. Council for Agr. Sci. and Tech. Task Force Rep. No. 129. Ames, Iowa.

Leonard, K.M., K.P. Reese, and J.W. Connelly. 2000. Distribution, movements and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildl. Biol. 6:265–270.

Lucchini, V., J. Hoglund, S. Klaus, J. Swenson, and Randi, E. 2001. Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. Molec. Phylogenetics and Evol. 20:149–162.

Lyon, L. J. and P.F. Stickney. 1976. Early vegetal succession following large Northern Rocky Mountain wildfires, p. 355–375. *In:* Proceedings, Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council, Fire and Land Management Symposium, Missoula, Mont., Tallahassee, Fla.

Mackie, R.J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20:1–79.

Martin, N.S. 1970. Sagebrush control related to habitat and sage grouse occurrence. J. Wildl. Manage. 34:313–320.

Martin, N.S. 1976. Life history and habitat requirements of sage grouse in relation to sagebrush treatment. Proc. of the West. Assoc. State Game & Fish Commissioners 56:289–294.

Martin, R.C. 1990. Sage grouse responses to wildfire in spring and summer habitats. M.S. Thesis, Univ. Ida. Moscow, Ida.

McDowell, M.K.D. 2000. The effects of burning in mountain big sagebrush on key sage grouse habitat characteristics in southeastern Oregon. M.S. Thesis, Ore. St. Univ. Corvallis, Ore.

Merritt, S., C. Prosser, K. Sedivec, and D. Bangsund. 2001. Multi-species grazing and leafy spurge. U.S.D.A.-ARS Team Leafy Spurge, Sidney, Mont.

Miller, R.F. and L.L. Eddleman. 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Ore. Agr. Exp. Sta. Bull. 151. Corvallis, Ore.

Miller, R.F. and J.A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. J. Range Manage. 52:550–559.

Miller, R.F. and R.J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis, p. 15–30. *In:* K.E.M. Galley and T.P. Wilson (eds.) Proc. Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Misc. Pub. No. 11, Tall Timbers Res. Sta. Tallahassee, Fla.

Miller, R.F., T. Svejcar, and J.A. Rose. 2000. Western juniper succession in shrub steppe: Impacts on community composition and structure. J. Range Manage. 53:574–585.

Miller, R.F., T.J. Svejcar, and N.E. West. 1994. Implications of livestock grazing in the Intermountain sagebrush region: plant composition, p. 101–146. *In:* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.) Ecological Implications of Livestock Herbivory in the West. Soc. for Range Manage. Denver, Colo.

Miller, R.F., J. Bates, K. Davis, and L. Ziegenhagen. 2003. Sagebrush cover: community level = sage grouse requirements**?** Proc. Society for Range Management Annual Meeting Casper, Wyo.

Mosley, J. C. 1996. Prescribed sheep grazing to suppress cheatgrass: A review. Sheep and Goat Res. J. 12:74-81.

Mosley, J.C., S.C. Bunting, and M.E. Manoukian. 1999. Cheatgrass, p. 175-188. *In*: R.L. Sheley and J.K. Petroff (eds.) Biology and Management of Noxious Rangeland Weeds. Ore. State Univ. Press, Corvallis.

Mosley, J.C., P.S. Cook, A.J. Griffis, and J. O'Laughlin. 1997. Guidelines for managing cattle grazing in riparian areas to protect water quality: Review of research and best management practices policy. Univ. Idaho For., Wildl. and Range Policy Analysis Group Rept. 15.

Mueggler, W.F. 1950. Effects of spring and fall grazing by sheep on vegetation of the upper Snake River plains. J. Range Manage. 3:308–315.

Muggler, W.F. and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA For. Ser Gen. Tech Rep. INT-66.

Myers, L.H. 1989. Grazing and riparian management in southwestern Montana, p. 117–120. *In*: R.E. Gresswell, B.A. Barton, and J.L. Kershner (eds.) Practical Approaches to Riparian Resource Management—An Educational Workshop, U.S.D.I.-B.L.M., BLM-MT-PT-89-001-4351.

Neel, L.A. 1980. Sage grouse response to grazing management in Nevada. M.S. Thesis, Univ. Nevada. Reno, Nev.

Nelson, O.C. 1955. A field study of the sage grouse in southeastern Oregon with special reference to reproduction and survival. M.S. Thesis. Ore. St. Univ. Corvallis, Ore.

Nelle, P.J., K.P. Reese, and J.W. Connelly. 2000. Long-term effects of fire on sage grouse habitat. J. Range Manage. 53:586–591.

Ngugi, K.R., J. Powell, F.C. Hinds, and R.A. Olson. 1992. Range animal diet composition in southcentral Wyoming. J. Range Manage. 45:542–545.

Oakleaf, R.J. 1971. Relationship of sage grouse to upland meadows in Nevada. M.S. Thesis, Univ. Nevada. Reno, Nev.

Olsen, F.W. and R.M. Hansen. 1977. Food relations of wild free-roaming horses to livestock and big game, Red Desert, Wyoming. J. Range Manage. 30:17–20.

Olson, B.E. and R.T. Wallander. 2001. Sheep grazing spotted knapweed and Idaho fescue. J. Range Manage. 54:25–30.

Olson, R.A. and T.D. Whitson. 1996. Improving wildlife habitat quality on sagebrush rangelands with Spike 20P herbicide. p. 7–13, *In:* Down To Earth. DowElanco, Indianapolis, Ind.

Olson, R.A. and T.D. Whitson. 2002. Restoring structure in late-successional sagebrush communities by thinning with tebuthiuron. Rest. Ecol. 10:146–155.

Olson, R.A., J. Hansen, and T.D. Whitson. 1996. Enhancing rangeland forage production and biodiversity with tebuthiuron, p. 55–59. *In:* K.E. Evans (ed.) Sharing Common Ground On Western Rangelands: Proc. of A Livestock/Big Game Symposium. February 26–28, 1996, Sparks, Nev. U.S.D.A. For. Serv., Gen. Tech Rept. INT-GTR-343.

Olson, R.A., J. Hansen, T.D. Whitson, and K. Johnson. 1994. Tebuthiuron to enhance rangeland diversity. Rangelands 16:197–201.

Orpet, J.E. and H.G. Fisser. 1979. Long-term effects of 2,4-D applications on big sagebrush. Proc. Soc. for Range Manage. p. 29.

Patterson, R.L. 1952. The sage grouse in Wyoming. Sage Books, Inc., Denver, Colo.

Payne, G.F. 1973. The effect of 2,4-D on sagebrush and associated vegetation on the Beaverhead National Forest, Montana. Final Report. U.S.D.A., For. Ser. Final Rept., Mont. Agr. Exp. Sta.

Pearson, L.C. 1964. Effect of harvest date on recovery of range grasses and shrubs. Agron. J. 56:80–82.

Pechanec, J.F. and G. Stewart. 1949. Grazing spring-fall sheep ranges of southern Idaho. U.S.D.A. Circ. 808.

Pechanec, J.F., G. Stewart, and J.P. Balisdell. 1954. Sagebrush burning – good and bad. U.S.D.A. Farmer's Bull. 1948.

Pellant, M. 1994. History and applications of the Intermountain greenstripping program, p. 63–68. *In*: S.B. Monsen and S.G. Kitchen (eds.) Proc. Ecology and Management of Annual Rangelands, U.S.D.A. For. Serv., Gen. Tech. Rept. INT-313.

Pellant, M., J. Kaltenecker, and S. Jirik. 1999. Use of OUST› herbicide to control cheatgrass in the Northern Great Basin, p. 322–326. *In:* S.B. Monsen and R. Stevens (compilers) Proc. Ecology and Management of Pinyon-Juniper Communities Within the Interior West. U.S.D.A. For. Serv., Gen. Tech. Rept. RMRS-P-9.

Peters, E.F. and S.C. Bunting. 1994. Fire conditions pre- and post- occurrence of annual grasses on the Snake River Plain, p. 31–36.

026515

In: S.B. Monsen and S.G. Kitchen (eds.) Proc. Ecology and Management of Annual Rangelands. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-313.

Petersen, B.E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. M.S. Thesis, Colo. St. Univ. Fort Collins, Colo.

Peterson, J.G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. J. Wildl. Manage. 34:147–155.

Potts, G.R. 1986. The partridge. Collins, London, England.

Pyle, W.H. 1993. Response of brood-rearing habitat of sage grouse to prescribed burning in Oregon. M.S. Thesis, Ore. St. Univ. Corvallis, Ore.

Pyle, W.H. and J.A. Crawford. 1996. Availability of foods of sage grouse chicks following prescribed burning in sagebrush-bitterbrush. J. Range Manage. 49:320–324.

Pyrah, D.B. 1971. Sage grouse habitat research in central Montana. Proc. West. Assoc. State Game and Fish Comm. 51:293–300.

Rasmussen, D.I. and L.A. Griner. 1938. Life history and management studies of the sage grouse in Utah, with special reference to nesting and feeding habits. Trans. North Amer. Wildl. Conf. 3:852–864.

Ratliff, R.D. and J.N. Reppert. 1974. Vigor of Idaho fescue grazed under rest-rotation and continuous grazing. J. Range Manage. 27:447–449.

Reiner, R. J. and P. J. Urness. 1982. Effect of grazing horses managed as manipulators of big

Rice, B. and M. Westoby. 1978. Vegetative responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. J. Range Manage. 31:28–34.

Riegel, G. M., R.F. Miller, S.E. Smith, and C. Skinner. (in press). The history and ecology of fire in Northeastern California. *In:* N.G. Sugihara, M. Borchert, J. van Wagtendonk, J. Fites-Kaufmann, and K. Shaffer (eds.) Fire and Vegetation Interactions in California Ecosystems. Univ. of Calif. Press, Berekeley, Calif.

Rich, T. 1985. Sage grouse population fluctuations: evidence for a 10-year cycle. U.S. Dep. Inter., Bur. Land Manage. Tech. Bull. 85-1. Boise, Ida.

Rickard, W.H., D.W. Uresk, and J.F. Cline. 1975. Impact of cattle grazing on three perennial grasses in southcentral Washington. J. Range Manage. 28:108–112.

Riggs, R.A. and P.J. Urness. 1989. Effects of goat browsing on Gambel oak communities in northern Utah. J. Range Manage 42:354–360.

Rowland, M.M. and W.J. Wisdom. 2002. Research problem analysis for greater sage-grouse in Oregon. Final report submitted to Ore. Dept. of Fish and Wildl.

Roberson, J.A. 1986. Sage grouse-sagebrush relationships: A review, p.157–167. *In*: E.D. McArthur, & B.L. Welch (eds.) Proc. of a Symposium on the Biology of *Artemisia* and *Chrysothamnus*. U.S.D.A. For Serv., Gen. Tech. Rept. INT-200.

Robertson, M.D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southeastern Idaho. M.S. Thesis, Univ. Ida. Moscow, Ida.

Rogers, G.E. 1964. Sage grouse investigations in Colorado. Colo. Game, Fish and Parks Dept. Tech. Pub. 16. Denver, Colo.

Sanders, K.D. 1998. Utilization standards: the quandary revisited, p. 2-8. *In:* Stubble height and utilization measurements: Uses and misuses. Ore. Agr. Exp. Sta. Bull. 682. Corvallis, Ore.

Sanders, K.D. and A.S. Voth. 1983. Ecological changes of grazed and ungrazed plant communities, p. 176–179. *In*: S.B. Monsen and N. Shaw (eds.) Managing Intermountain Rangelands - Improvement of Range and Wildlife Habitats. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-157.

Savage, D.E. 1969. Relation of sage grouse to upland meadows in Nevada. Nev. Fish and Game Comm., Job Completion Rept., Proj. W-39-R, Job 12, Reno, Nev.

Schoenberg, T.J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. M.S. Thesis, Colo. St. Univ. Fort Collins, Colo.

Schneegas, E.R. 1967. Sage grouse and sagebrush control. Trans. N. Amer. Wildl. Conf. 32:270–274.

Schroeder, M.A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in northcentral Washington. Condor 99:933–941.

Schroeder, M. A. and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildl. Soc. Bull. 29:24–32.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*), p. 1–28. *In:* A. Poole and F. Gill (eds.) The birds of North America. The Birds of North America, Inc., Philadelphia, Penn.

Scott, J.W. 1942. Mating behavior of the sage grouse. Auk 59:477–498.

Severson, K., M. May, and W Hepworth. 1968. Food preferences, carrying capacities, and forage competition between antelope and domestic sheep in Wyoming's Red Desert. Univ. Wyo. Agr. Exp. Sta. Sci. Monogr. 10.

Sharp, L., K. Sanders, and N. Rimbey. 1994. Management decisions based on utilization: Is it really management? Rangelands 16:38–40.

Shaw, N.L. 1992. Recruitment and growth of Pacific willow and sandbar willow seedlings in response to season and intensity of cattle grazing, p. 130–137. *In*: W.P. Clary, E.D. McArthur, D. Bedunah, and C.L. Wambolt (eds.) Proc. Symp. on Ecology and Management of Riparian Shrub Communities. U.S.D.A. For. Serv., Gen. Tech. Rept. INT-289.

Shrader-Frechette, K.S. and E.D. McCoy. 1993. Method in Ecology: Strategies for Conservation. Cambridge Univ. Press, New York.

Smith, M.A., J.C. Malechek and K.O. Fulgham. 1979. Forage selection by mule deer on winter range grazed by sheep in spring. J. Range Manage. 32:40–45.

Stewart, G. and A.C. Hull. 1949. Cheatgrass (*Bromus tectorum*) - an ecologic intruder in southern Idaho. Ecol. 30:58–74.

Sveum, C.M., J.A. Crawford, and W.D. Edge. 1998a. Use and selection of brood-rearing habitat by sage grouse in southcentral Washington. Great Basin Nat. 58:344–351.

Sveum, C.M., W.D. Edge, and J.A. Crawford. 1998b. Nesting habitat selection by sage grouse in southcentral Washington. J. Range Manage. 51:265–269.

Swetnam, T.W., C.D. Allen, and J.L. Betancourt. 1999. Applied historical ecology: Using the past to manage the future. Ecol. Appl. 9:1189–1206.

Tate, J. Jr., M.S. Boyce, and T.R. Smith. 1979. Response of sage grouse to artificially created display ground, p. 459-463. *In:* G.A. Swanson (tech-co-ord) The mitigation symposium. U.S.D.A., For. Serv., Gen Tech. Rep RM-65.

Tausch, R.J. 1999. Transitions and thresholds: influences and implications for management in pinyon and Utah juniper woodlands, p.361–365. *In:* Monsen, S.B., R. Stevens, R.J. Tausch, R. Miller, S. Goodrich (eds.) Proceedings of the Ecology and management of pinyon-juniper communities within the interior west, Sept. 15–18, 1997. U.S.D.A. For. Serv. RMRS-P-9.

Tisdale, E.W., M. Hironaka, and M.A. Fosberg. 1965. An area of pristine vegetation in Craters of the Moon National Monument, Idaho. Ecology 46:349-352.

Turner, M. G., R.H. Gardner and R.V. O'Neill. 2001. Landscape Ecology in Theory and Practice. Springer Verlag, New York, N.Y.

Trueblood, R.W. 1954. The effect of grass reseeding in sagebrush lands on Sage Grouse Populations. M.S. Thesis, Ut. St. Agr. Coll., Logan, Ut.

Uresk, D.W. and W.H. Rickard. 1976. The abortifacient and toxic effects of big sagebrush (*Artemisia tridentata*) and juniper (*Juniperus osteosperma*) on domestic sheep. J. Range Manage. 29:278–280.

USDI-BLM. 1990. State of the public rangelands, 1990. Bur. of Land Manage., U.S. Dept. of Interior, Washington, D.C.

Vale, T.R. 1974. Sagebrush conversion projects: An element of contemporary environmental change in the western United States. Biol. Conserv. 6:274–284.

Volland, L.A. and J.D. Dell. 1981. Fire effects on Pacific Northwest forest and range vegetation. U.S.D.A. For. Serv. Region 6, Portland, Ore.

Wagner, F.H. 1978. Livestock grazing and the livestock industry, p. 121-145. *In:* H. Brokaw (ed.), Wildlife in America. Council on Environmental Qual., Wash. D.C.

Waichler, W.S., R.F. Miller, and P.S. Doescher. 2001. Community characteristics of old-growth western juniper woodlands. J. Range Manage. 54:518–527.

Wakkinen, W.L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. M.S. Thesis, Univ. Ida. Moscow, Ida.

026516

Wakkinen, W.L., K.P. Reese, and J.W. Connelly. 1992. Sage grouse nest locations in relation to leks. J. Wildl. Manage. 56:381–383.

Wallestad, R.O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. J. Wildl. Manage. 35:129–136.

Wallestad, R.O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Dept. Fish, Game, and Parks. Helena, Mont.

Wallestad, R.O. and D.B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. J. Wildl. Manage. 38:630–633.

Wallestad, R.O., J.G. Peterson, and R.L. Eng. 1975. Foods of adult sage grouse in central Montana. J. Wildl. Manage. 39:628–630.

Waltenberger, D.W., W.S. Belles, and G.A. Lee. 1979. The control of big sagebrush on central Idaho rangeland. Proc. West. Soc. Weed Sci. p. 77.

Wambolt, C.L. and G.F. Payne. 1986. An 18-year comparison of control methods for Wyoming big sagebrush in southwestern Montana. J. Range Manage. 39:314–319.

Wambolt, C.L., K.S. Walhof, and M.R. Frisina. 2001. Recovery of big sagebrush communities after burning in south-western Montana. J. Environ. Manage. 61:243–252.

Washington-Allen, R.A. 2003. Retrospective ecological risk assessment of rangeland health using multi-temporal satellite imagery. PhD Diss., Utah State Univ., Logan, Ut.

Watts, M.J. and C.L. Wambolt. 1996. Long-term recovery of Wyoming big sagebrush after four treatments. J. Environ. Manage. 46:95–105.

West, N.E. 1983a. Great Basin-Colorado Plateau sagebrush semi-desert, p. 331-349. *In:* N.E. West (ed.) Temperate Deserts and Semideserts. Vol. 5. Ecosystems of the World, Elsevier, Amsterdam.

West, N.E. 1983b. Western Intermountain sagebrush steppe, p. 351-374. *In:* N.E. West (ed.) Temperate Deserts and Semideserts. Vol. 5. Ecosystems of the World, Elsevier, Amsterdam.

West, N.E. 1989. Vegetation types of Utah, p. 18-56. *In:* K.L. Johnson, (ed.) Rangeland resources of Utah. Coop Ext. Serv. Pub., Ut. St. Univ., Logan.

West, N.E. 1999a. Juniper-pinon savannas and woodlands of western North America, p. 284-301. *In:* R.C. Anderson, J.S. Fralish and J.M. Baskin (eds.) Savannas, Barrens, and Rock outcrop Plant Communities of North America. Cambridge Univ. Press, New York.

West, N.E. 1999b. Managing for biodiversity of rangelands, p. 101–126. *In*: W.W. Collins and C.O. Qualset (eds.) Biodiversity in Agrosystems. CRC Press, Boca Raton, Fla.

West, N.E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems, p.15–26. *In:* Entwistle, P.G., A.M. Debolt, J.H. Kaltenecker and K. Steenhof (compilers) Proc. Sagebrush Steppe Ecosystems Symposium. Bureau of Land Mgt. Publ. No. BLM/ID/PT-0011001+1150.

West, N.E. and N.S. Van Pelt. 1986. Successional patterns in pinyon-juniper woodlands, p. 43–52. *In:* Everett, R.L. (ed.) Proc. Pinyon-juniper conference. U.S.D.A. For. Serv. Gen. Tech. Rept. INT-215.

West, N.E. and T.P. Yorks. 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. J. Range Manage. 55:171–181.

West, N.E. and J. A. Young. 2000. Vegetation of Intermountain valleys and lower mountain slopes, p. 255–284. *In:* M.A. Barbour and W.D. Billings (eds) North American Terrestrial Vegetation 2nd ed. Cambridge Univ. Press, New York, N.Y.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42:266–274.

Whitson, T. D. 2003. The effects of Plateau (Imazapic) on dalmatian toadflax, downy brome, Russian knapweed and perennial pepperweed. Proc. Soc. for Range Manage. Annual Meet. Casper, Wyo.

Whitson, T. D. and H. P. Alley. 1984. Tebuthiuron effects on *Artemisia* spp. and associated grasses. Weed Sci. 32:180–184.

Whitson, T. D., M. A. Ferrell, and H. P. Alley. 1988. Changes in rangeland canopy seven years after tebuthiuron application. Weed Tech. 2:486–489.

Whisenant, S.G. 1990. Changing fire frequencies on Idaho's River Plains: ecological and management implications, p. 4–10. *In:* Proc. Cheatgrass invasion shrub die-off, and other aspects of shrub biology and management. U.S.D.A. For. Serv. Tech. Rept. INT-276.

Winward, A.H. 1970. Taxonomic and ecological relationships of the big sagebrush complex in Idaho. Ph.D. Diss, Univ. of Ida., Moscow, Ida.

Winward, A.H. 1991. A renewed commitment to management of sagebrush grasslands, p. 2-7. *In*: Miller, R.F. (ed.) Management in the sagebrush steppe. Agr. Exp. Sta. Spec. Rpt. 880. Ore. St. Univ. Corvallis, Ore.

Winward A.H. 2000. Monitoring the vegetation resources in riparian areas. USDA For. Serv. Gen. Tech. Rept. RMRS-47.

Wisdom, M. J., M. M. Rowland, B.C. Wales, M. A. Hemstrom, W. J. Hann, M. G. Raphael, R.S. Holthausen, R.A. Gravenmier, and T.D. Rich. 2002. Modeled effects of sagebrush steppe restoration on greater sage-grouse in the Interior Columbia Basin, U.S.A. Cons. Biol.16:1223–1231.

Woodward A.J. and S.D. Fuhlendorf. 2001 Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. Amer. Mid. Natural.145:261–274.

Wright, H.A. 1970. Response of big sagebrush and three-tip sagebrush to season of clipping. J. Range Manage. 23:20–22.

Wright, H. A. and A. W. Bailey. 1982. Fire Ecology: United States and southern Canada. John Wiley and Sons, New York, N.Y.

Wright, H.A. and J.O. Klemmedson. 1965. Effects of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology 46:680–688.

Wright, H.A., L.F. Neuenschwander, and C. M. Britton. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities: A state-of-the-art review. U.S.D.A. For. Serv. Gen. Tech. Rept. INT-58.

Wright, J.C. and E.A. Wright. 1948. Grassland types of southcentral Montana. Ecology 29:449-460.

Wrobleski, D.W. 1999. Effects of prescribed fire on Wyoming big sagebrush communities: Implications for ecological restoration of sage grouse habitat. M.S. Thesis. Ore. St. Univ. Corvallis, Ore.

Young, J. A. and R. A. Evans. 1973. Downy brome - intruder in the plant succession of big sagebrush communities in the Great Basin. J. Range Manage. 26:410–415.

Young, J.A. and R.A. Evans. 1974. Population dynamics of green rabbitbrush in disturbed big sagebrush communities. J. Range. Manage. 27: 127–132

Young, J.A. and B.A. Sparks. 1985. Cattle in the cold desert. Ut. State Univ. Press, Logan, Utah.

Young, J.A, R.A. Evans, and J. Major. 1972. Alien plants in the great basin. J. Range Manage. 25:194-201.

Young, J.A., R.A. Evans, and P.T. Tueller. 1976. Great Basin plant communities-pristine and grazed, p. 187-215. *In:* R. Elston and P. Headrick (eds.) Holocene environmental change in the Great Basin. Nev. Arch. Survey, Res. Paper No. 6, Univ. of Nev., Reno. 5:194–201

Young, J.R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. Ph.D. Thesis, Purdue Univ. West Lafayatte, Ind.

Young, R.P. and R.F. Miller. 1985. Response of *Sitanion hystrix* (Nutt.) J.G. to prescribed burning. Amer. Midl. Natur. 113:182–87.

Zablan, M.A. 1993. Evaluation of sage grouse banding program in North Park, Colorado. M.S. Thesis, Colo. St. Univ. Fort Collins, Colo.

026517

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 477–488
DOI: 10.1650/CONDOR-15-165.1

RESEARCH ARTICLE

Declining recruitment of Gunnison Sage-Grouse highlights the need to monitor juvenile survival

Amy J. Davis,[1a#]* Michael L. Phillips,[2#] and Paul F. Doherty, Jr.[1]

[1] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA
[2] Colorado Parks and Wildlife, Fort Collins, Colorado, USA
[a] Current address: U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Fort Collins, Colorado, USA
[#] These authors contributed equally to the paper
* Corresponding author: Amy.J.Davis@aphis.usda.gov

Submitted September 24, 2015; Accepted April 5, 2016; Published June 2, 2016

ABSTRACT

Recruitment of juveniles is an important vital rate that influences population growth and is fundamental to understanding trends in population size. Estimates of recruitment are often focused on the period just after hatching (prefledgling stage), which is typically the lowest survival period and often the most variable. Few studies examine true recruitment—survival from hatching to entering the breeding population—although this information is more relevant to understanding population trends. We studied the recruitment of Gunnison Sage-Grouse (*Centrocercus minimus*), a federally threatened species in the U.S., to examine the relative importance of chick and juvenile survival to recruitment patterns. We evaluated recruitment from 2005 to 2010 by combining separate estimates of chick survival (hatching to 30 days of age) and juvenile survival (31 days of age to the start of the first breeding season). To explain variation in these survival rates, we examined the effects of population, individual (i.e. age), and temporal (within-year and among-year differences) factors associated with recruitment of Gunnison Sage-Grouse. The factors that most explained juvenile survival rates were temporal (among-year trends and within-year seasonal effects). Chick survival rates varied by population, and daily chick survival increased with chick age. We found a slight negative trend in chick survival and a strong negative trend in juvenile survival from 2005 to 2010. The overall recruitment rate declined from 0.32 (± 0.09 SE) in 2005 to 0.04 (± 0.03 SE) in 2010. This decline coincided with a decline observed in population index data, which was not reflected in other demographic data. If survival had not been monitored past 30 days of age, estimates of recruitment would have remained relatively stable. This work highlights the importance of monitoring juvenile survival, as it may influence population dynamics.

Keywords: Centrocercus minimus, chick survival, Gunnison Sage-Grouse, juvenile recruitment, population trends

La disminución del reclutamiento en *Centrocercus minimus* resalta la necesidad de monitorear la supervivencia de los individuos jóvenes

RESUMEN

El reclutamiento de individuos jóvenes es una tasa vital importante que influye sobre el crecimiento poblacional y es fundamental para entender las tendencias en el tamaño poblacional. Los estimados del reclutamiento generalmente se enfocan en el periodo justo después de la eclosión (prefledgling etapa), que es típicamente el periodo de menor supervivencia y a menudo el más variable. Pocos estudios examinan el reclutamiento real –supervivencia desde la eclosión hasta la entrada a la población reproductiva– aunque esta información es más relevante para entender las tendencias poblacionales. Estudiamos el reclutamiento en *Centrocercus minimus*, una especie federalmente amenazada en los Estados Unidos, para examinar la importancia relativa de la supervivencia de polluelos e individuos jóvenes en la evaluación de los patrones de reclutamiento. Evaluamos el reclutamiento entre 2005 y 2010 combinando estimados separados de la supervivencia de los polluelos (hasta 30 días de edad) y de los jóvenes (31 días de edad hasta el comienzo de la primera temporada reproductiva). Para explicar la variación en estas tasas de supervivencia, examinamos los efectos de factores poblacionales, individuales (i.e. edad) y temporales (diferencias dentro y entre años) asociados con el reclutamiento en *C. minimus*. Los factores que mejor explicaron las tasas de supervivencia de los jóvenes fueron los temporales (tendencia entre años y efectos estacionales en un año). Encontramos una tendencia ligeramente negativa en la supervivencia de los polluelos y una fuerte tendencia negativa en la supervivencia de los jóvenes entre 2005 y 2010. La tasa general de reclutamiento disminuyó de 0.32 (DE 0.09) en 2005 a 0.04 (DE 0.03) en 2010. Este declive coincide con los observados en los índices de datos de la población, que no se reflejaron en otros datos demográficos. Si la supervivencia no se hubiese monitoreado pasados los 30 días de edad, los estimados del reclutamiento habrían permanecido relativamente estables. Este trabajo resalta la importancia de monitorear la supervivencia de los jóvenes ya que ésta puede influir en la dinámica poblacional.

© 2016 Cooper Ornithological Society. ISSN 0010-5422, electronic ISSN 1938-5129
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at aoucospubs@gmail.com

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

Palabras clave: Centrocercus minimus, supervivencia de polluelos, reclutamiento de jóvenes, tendencias poblacionales

INTRODUCTION

Successful conservation and management of species require accurate information about factors contributing to population declines. Effective management is particularly necessary for rare or declining species. Life-history theory often enables us to determine which vital rates are most likely to influence population growth rates (Pfister 1998). Generally, for longer-lived species, population change is most sensitive to adult survival than other vital rates, and, for short-lived species, population change is more sensitive to reproductive success (Heppell et al. 2000, Sæther and Bakke 2000). For many bird species, recruitment (the proportion of birds hatched that survive to join the breeding population) is a primary driver of population growth (e.g., Roff 1992). Detecting changes in recruitment across time may be fundamental to understanding trends in population growth of bird species.

Recruitment can be thought of as comprising a prefledging stage (dependence on parental care for survival; henceforth, 'chick stage') and a postfledging stage (relative independence from parents; henceforth, 'juvenile stage'). It is generally more feasible to study the chick stage due to the dependence on parental care and the localized nature of brood rearing. Juvenile survival (survival from fledging until joining the breeding population) is often more difficult to study because birds disperse or migrate and are no longer reliant on parental care. Therefore, more studies focus on the earlier stage than the latter (e.g., Hannon and Martin 2006, Taylor et al. 2012). However, it is important to consider each of these stages when estimating recruitment. Accurately estimating vital rates is particularly important for species of conservation concern, because population projections and growth rates based on vital rate estimates are used for conservation and management planning, including listing decisions. Resulting population assessments may be biased, and management decisions misguided, if vital rates are not estimated accurately.

The relationship between vital rates and population growth is known to vary among species (Sæther and Bakke 2000). However, this relationship also may vary among different populations within the same species (Johnson et al. 2010). These varying relationships might indicate that different management strategies are necessary to most efficiently manage separate populations (Johnson et al. 2010). Under these conditions, evaluating vital rates, such as recruitment in birds, for different populations within a species is necessary.

Gunnison Sage-Grouse (*Centrocercus minimus*) is listed as Threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2014) and its population has declined substantially concomitant with a contraction of its range (Schroeder et al. 2004). Recruitment has been proposed as the most limiting demographic parameter for population growth of sage-grouse species (Connelly et al. 2004, Gunnison Sage-Grouse Rangewide Steering Committee 2005, Gregg and Crawford 2009). Historical population projections for Gunnison Sage-Grouse relied on information from the related Greater Sage-Grouse (*Centrocercus urophasianus*) to fill in gaps where information for Gunnison Sage-Grouse did not exist (Gunnison Sage-Grouse Rangewide Steering Committee 2005). Thus, determining survival estimates and how these rates may be changing over time is critical for Gunnison Sage-Grouse. Distinguishing between annual variability and trends across time is particularly important for developing more accurate population projections for Gunnison Sage-Grouse.

Our goals were to estimate recruitment for Gunnison Sage-Grouse, to evaluate how this rate may be changing over time, and to assess differences among populations of Gunnison Sage-Grouse. To be able to compare our estimates of recruitment with estimates for Greater Sage-Grouse, we estimated chick survival (hatching to 30 days of age) on a daily scale and juvenile survival (31 days of age until the start of the first breeding season) on a monthly scale. We determined the influence of individual (age of the chick, age of the mother) and within-year (timing of hatching or seasonal variation) factors on survival. Our study provides crucial information for an understanding of Gunnison Sage-Grouse population dynamics, which is necessary for implementing effective conservation strategies and management actions.

METHODS

Study Areas

Our research was conducted primarily on federal land (Bureau of Land Management and Forest Service), but also on some private land with permission. Our study area encompassed 2 of 7 isolated populations of Gunnison Sage-Grouse, the Gunnison Basin and San Miguel populations. The Gunnison Basin population held 85%–90% of all Gunnison Sage-Grouse (Gunnison Sage-Grouse Rangewide Steering Committee 2005). This population resides in the Gunnison Basin, in Gunnison and Saguache counties, Colorado, USA (Figure 1). The Gunnison Basin is an intermontane basin, 2,000 km^2 in size, ranging in elevation from 2,300 to 2,900 m (Hupp and Braun 1989). Mountainous terrain borders the northern, eastern, and

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

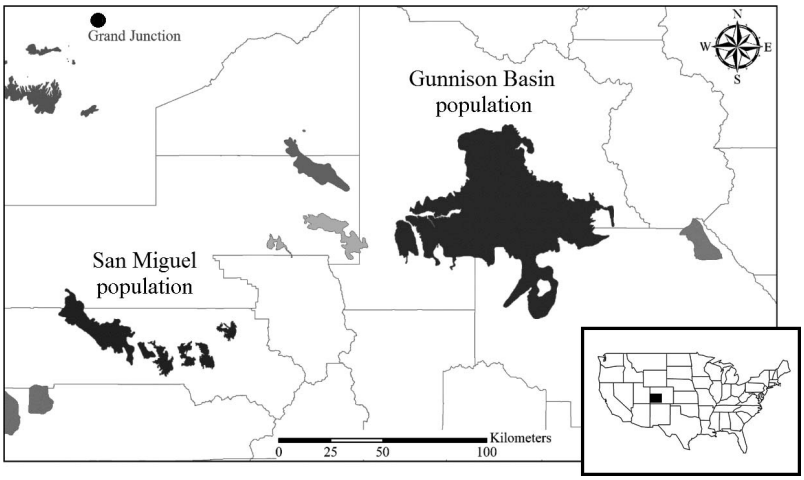


FIGURE 1. Distribution of Gunnison Sage-Grouse in Colorado, USA, in 7 isolated populations. We studied the 2 darkest-shaded populations (Gunnison Basin and San Miguel).

southeastern sides of this basin, and these areas contain habitat not commonly used by sage-grouse (Connelly et al. 2000). The San Miguel population was the second-largest population (containing 3% of all Gunnison Sage-Grouse; Gunnison Sage-Grouse Rangewide Steering Committee 2005). The San Miguel study population was located in Montrose and San Miguel counties, Colorado, USA. It was comprised of 6 interconnected subpopulations spread over an area of 400 km^2. The elevation of this area ranges from 1,900 to 2,800 m (Gunnison Sage-Grouse Rangewide Steering Committee 2005).

The habitat for both populations was predominately sagebrush steppe dominated by sagebrush (*Artemisia* spp.). The Gunnison Basin was dominated by mountain big sagebrush (*A. tridentate vaseyena*) interspersed with rabbitbrush (*Chrysothamnus* spp.), antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier* spp.), and mountain snowberry (*Symphoricarpos oreophilus*). Black sagebrush (*A. nova*) was found on xeric ridgetops and south-facing slopes (Hupp and Braun 1989, Gunnison Sage-Grouse Rangewide Steering Committee 2005). The shrubs in San Miguel county were predominately little sagebrush (*A. arbuscula*) and black sagebrush, with some mountain big sagebrush along drainages (Gunnison Sage-Grouse Rangewide Steering Committee 2005, Stiver et al. 2008).

Capture and Monitoring

We used spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) to trap female Gunnison Sage-Grouse from mid-March through early May, 2005–2010. Captured Gunnison Sage-Grouse were fitted with a 17 g necklace-style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a numbered leg band (National Band & Tag Company, Newport, Kentucky, USA). The transmitter weight was <2% of average adult female Gunnison Sage-Grouse body weight (1,270 g ± 90 g SD). We weighed each bird and used plumage characteristics to determine age (Beck et al. 1975). Each Gunnison Sage-Grouse was categorized as either ASY (≥2 yr old; second breeding season or later) or SY (≤1 yr old; first breeding season).

We monitored females 6 days a week throughout the breeding season to determine nesting status (see Davis et al. 2015b for nest monitoring details). For every successful nest (at least 1 egg hatched), chicks were caught and radio-tagged within 48 hr of hatching. We captured chicks by locating and flushing the hen while she was brooding the young (just after dawn or just before dusk). We did not trap in inclement weather (i.e. rain or snow, or temperatures lower than −7°C). Chicks were placed in a lidded plastic tub with a hot water bottle for warmth during handling. We weighed all chicks and marked half of the brood (up to 3 individuals) with 1 g radio-transmitters (Advanced Telemetry Systems) that had a battery life of 18 days. Transmitters were attached with sutures (Burkepile et al. 2002). The transmitter weight was <4% of a Gunnison Sage-Grouse chick's body weight. Based on the 4% maximum, we did not place transmitters on chicks weighing <23 g (<2% of all chicks encountered, and none in the San Miguel population, were too light to tag). Using telemetry, we ensured that the hen was ≤20 m away before releasing her chicks.

We recaptured chicks 2 weeks after hatching and replaced the 1 g transmitters with 4 g transmitters (Advanced Telemetry Systems), also attached with sutures. The 4 g transmitters had a 6 mo battery life. Six chicks that weighed <80 g at recapture were tagged with another 1 g

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

transmitter, as the 4 g transmitter would have been >5% of the bird's weight. We recaptured these 6 birds within 18 days to replace the smaller transmitters with 4 g transmitters (each of these chicks survived to 30 days of age). We recaptured all birds in September or October and replaced the 4 g transmitters with 17 g necklace-style radio-transmitters (Advanced Telemetry Systems) if birds weighed >340 g (ensuring that the transmitter was not >5% of the bird's weight); if a bird weighed <340 g, we fit a new 4 g transmitter.

We located chicks 6 days a week for the first 60 days using ground triangulation. Between 60 and 120 days of age, chicks were located 3–4 times a week by triangulation. Aerial locations were obtained monthly during the fall and winter. Chick transmitters (1 g and 4 g) did not have mortality sensors. If a chick was located without the hen, visual observation was used to determine whether or not the chick was alive. We determined mortality of birds based on direct observation or transmitter mortality sensors.

Statistical Analysis

We ran 2 separate analyses, a daily survival analysis for chicks up to 30 days of age (chick survival), and a monthly survival analysis for chicks 30 days old through 31 March (juvenile survival). We used these time frames both based on the survival curves of previous work on Greater Sage-Grouse and to allow for ease of comparison with studies on Greater Sage-Grouse. For both the chick survival and juvenile survival analyses we used the nest survival models (Dinsmore et al. 2002, Anthony and Willis 2009) in Program MARK (White and Burnham 1999). These models allow for staggered entry (Pollock et al. 1989) and are ideal for radio-telemetry studies. Birds that disappeared or slipped their collars were included as alive in the study area until their last encounter, then were censored from the study. Additionally, we censored any birds that might have been affected by handling (i.e. died within 24 hr of release).

We examined several of the same hypotheses for both the chick and juvenile survival analyses. These included comparing survival between the 2 populations (Population), determining whether survival fluctuated among years (Year), determining whether survival declined or increased across years (Trend), and testing whether seasonal timing of hatching improved survival rates (Hatch). For the chick survival analysis, we also tested whether daily survival rates increased with chick age (Age) and whether chicks of ASY hens had higher survival than those of SY hens (Hen age). For the juvenile survival analysis, we considered 2 within-year seasonal variation intervals. First, we considered whether survival varied from month to month throughout the year (Month). Second, we modeled within-year survival as being similar to the pattern of within-year ASY survival found for Gunnison Sage-Grouse (Davis et al. 2015a). This second model (Season) partitioned the year into seasons: brood rearing (May–July), late summer and fall (August–October), and nonbreeding (November–March).

To compare the relative importance of each model, we evaluated Akaike's Information Criterion with the small sample size correction factor (AIC_c; Burnham and Anderson 2002). We ran all combinations of factors, following the recommendations of Doherty et al. (2012). To evaluate the relative importance of each individual factor, we calculated its cumulative Akaike weight (w_i; Burnham and Anderson 2002). This information-theoretic approach allowed us to compare the strength of support for each covariate (larger values suggest strong support, while small values indicate weak support). An adapted cutoff of cumulative w_i above 0.5 has been used to indicate importance (Barbieri and Berger 2004), and we used this cutoff as a guide in our analyses.

We calculated 30-day chick survival and juvenile survival by multiplying the daily or monthly survival rates within each yearly period (Seber 1982, Powell 2007). To calculate an estimate of recruitment (survival from hatching to the first breeding season), we multiplied the chick and the juvenile survival rates (accounting for staggered entry into the analysis; Seber 1982, Powell 2007). Variances for derived estimates were calculated using the delta method (Powell 2007).

Bootstrap Analysis

We used a data bootstrap analysis to test for variability in the data that was greater than expected due to a lack of independence among individuals owing to sibling dependence (overdispersion). We followed methodologies described by Bishop et al. (2008) and implemented in Program MARK (White and Burnham 1999). Each bootstrap analysis consisted of 2,000 replicates. We resampled broods (not individual chicks) with replacement. The number of broods sampled equaled the number of broods in the original analysis; however, as different broods were randomly selected each time, the total number of chicks in the analysis varied with each sample. We ran the survival analysis for the most parameterized model in the analysis described above on each of the bootstrap replicates (model with year, age, population, hatch, and hen age for chick analysis; and model with month, year, and hatch for juvenile analysis). We then calculated the mean and standard deviation of survival estimates from the 2,000 bootstrap replicates. We estimated overdispersion in the dataset as the ratio of the bootstrap estimate of standard deviation ($[SD(\hat{S})]$) over the standard error from the survival estimate of the top model. Dependence among the broods was reflected in the standard deviation of the survival estimates. Burnham and

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

TABLE 1. The models that were most supported (within 2 Quasi–Akaike's Information Criterion of the top model [$\Delta QAIC_c$]) from the candidate model set (Appendix Table 5) for chick survival of Gunnison Sage-Grouse from the Gunnison Basin (2005–2010) and San Miguel (2007–2010) populations, Colorado, USA. The intercept-only model is shown for comparison. *K* is the number of parameters in the model, and w_i is the model weight.

Model [a]	$\Delta QAIC_c$	w_i	*K*	Deviance
Trend + Age + Population	0.000 [b]	0.139	4	444.232
Age + Population	0.186	0.127	3	446.422
Trend + Population	0.511	0.108	3	446.747
Population	0.632	0.101	2	448.870
Trend + Hatch + Age + Population	1.875	0.054	5	444.021
Age + Population + Hen age	1.952	0.052	4	446.184
Trend + Hen age + Age + Population	1.996	0.051	5	444.223
Intercept only	7.511	0.003	1	457.751

[a] 'Trend' represents a linear trend across years ($K = 1$); 'Age' represents a linear trend on the age of the chick from 1 to 30 days of age ($K = 1$); 'Population' represents Gunnison Basin if it is a 0 and San Miguel if it is a 1 ($K = 1$); 'Hatch' represents a linear trend based on the week in which the chick was hatched ($K = 1$); and 'Hen age' denotes the age of the hen: 0 for SY ($\leq$1 yr old) and 1 for ASY ($\geq$2 yr old; $K = 1$).
[b] The $QAIC_c$ value for the top model = 452.24.

Anderson (2002) suggest that estimates of the overdispersion parameter ($\hat{c}$) that are just above 1.0 show only slight overdispersion and that judgment should be used for interpretation. We interpreted estimates of $\hat{c} < 1.2$ to indicate weak support for overdispersion in the chick survival and juvenile survival analyses (Bishop et al. 2008). If the resulting $\hat{c}$ estimate was above the cutoff of 1.2, then the estimated $\hat{c}$ was incorporated into Program MARK and model estimates were compared using Quasi–Akaike's Information Criterion ($QAIC_c$; Burnham and Anderson 2002).

RESULTS

From 2005 to 2010, 134 females with broods were monitored and 328 chicks were marked. During the 6 study years, 15 chicks were found dead the day after capture at the capture site (all from the Gunnison Basin population). These birds may have died due to exposure after handling or they may have been more susceptible to predation after handling; regardless, they were censored from the study. Birds that could not be aged accurately were not included in the chick survival analysis. These included chicks that had been adopted by a marked hen (determined by an obvious size difference from their brood mates) and chicks whose hatch date was unknown ($n = 19$). Additionally, 4 chicks were not included in our analysis as they were used as a part of a separate study. This resulted in 290 chicks being included in the chick survival analysis. Eighty-seven birds were included in the juvenile survival analysis. Only 9 chicks from 4 broods were caught in the San Miguel population. One of these chicks was unable to be aged as it was considerably larger than the brood that it was caught with and thus was not included in the chick survival analysis. None of the 9 chicks survived to 30 days of age, and therefore no birds from the San Miguel population were included in the juvenile survival analysis. We also observed brood-mixing occurring during our study (e.g., hens with chicks of different sizes, chicks of hens that died being adopted by another hen, broods of one hen splitting to be with different hens).

Chick Survival Analysis

The bootstrap analysis was run on the most parameterized model (10 parameters). The estimate of $\hat{c}$ based on the ratio of the average bootstrap standard deviation over the standard error from the estimate of the full model was 2.036. This value was above 1.2, suggesting that a lack of independence existed in the data. Therefore, we used $QAIC_c$ to compare models.

Our model set consisted of 48 models (Appendix Table 5). Seven models were within 2 $QAIC_c$ points of the top model (typical cutoff for strongly supported models; Burnham and Anderson 2002). Since model uncertainty existed among the top 7 models, we used model averaging to estimate survival rates. 'Population' was included in all of these models (Table 1). Correspondingly, the cumulative w_i for a population effect was high (0.950; Table 2). Mean chick survival in the Gunnison Basin was 0.48 $\pm$ 0.11 SE, which was considerably higher than that of 0.01 $\pm$ 0.11 SE for the small sample ($n = 8$) from the San Miguel population. Despite the small sample, had survival rates been the same in the Gunnison Basin and San Miguel populations (i.e. 0.48), the probability of observing 0 of 8 chicks survive = 0.6%. Even accounting for sibling dependence and mortality of all 4 broods, the probability of the San Miguel population having had a survival rate of 0.48 was only ~7%.

There was marginal support for daily chick survival increasing with chick age, based on a cumulative w_i of 0.566 (Table 2). However, the estimated relationship was near 0 and the 95% confidence interval overlapped zero ($\hat{\beta} = 0.026$, 95% CL = –0.007, 0.059; estimates are on the logit scale). The cumulative w_i for the trend effect was just under the 0.5 cutoff. However, this parameter was included in fewer models than other parameters because it could not be in models with the year effect, and thus its importance might have been underestimated. This fact, coupled with our interest in evaluating changes in chick survival across time, led us to examine the trend effect further. The model-averaged estimates of annual chick survival suggested a slight downward trend, but the

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

TABLE 2. Cumulative covariate weights (w_i) for chick survival and juvenile survival analyses for Gunnison Sage-Grouse in the Gunnison Basin (2005–2010) and San Miguel (2007–2010) populations, Colorado, USA. The chick survival analysis was adjusted for overdispersion based on sibling dependence ($\hat{c} = 2.036$), and therefore the cumulative covariate weight was based on Quasi–Akaike's Information Criterion ($QAIC_c$). The juvenile survival analysis did not suggest that there was overdispersion and thus models were evaluated with Akaike's Information Criterion corrected for small sample size (AIC_c). Cumulative w_i above 0.50 are considered important.

Covariate [a]	Cumulative w_i	Number of models
Chick survival		
Population	0.950	24
Age	0.566	24
Trend	0.494	16
Hen age	0.281	24
Hatch	0.275	24
Year	0.042	16
Juvenile survival		
Season	0.998	6
Trend	0.791	6
Hatch	0.332	9
Year	0.188	6
Month	0.002	6

[a] 'Population' represents Gunnison Basin if it is a 0 and San Miguel if it is a 1; 'Age' represents a linear trend on the age of the chick from 1 to 30 days of age; 'Trend' represents a linear trend across years; 'Hen age' denotes the age of the hen: 0 for SY (≤1 yr old) and 1 for ASY (≥2 yr old); 'Hatch' represents a linear trend based on the week in which the chick was hatched; 'Year' denotes a separate parameter for each year in the study allowing for annual variability; 'Season' denotes parameterization that allows monthly survival to vary by brood-rearing period (May–July), late summer and fall (August–October), and nonbreeding period (November–March); and 'Month' denotes parameterization that allows for full monthly variability in survival.

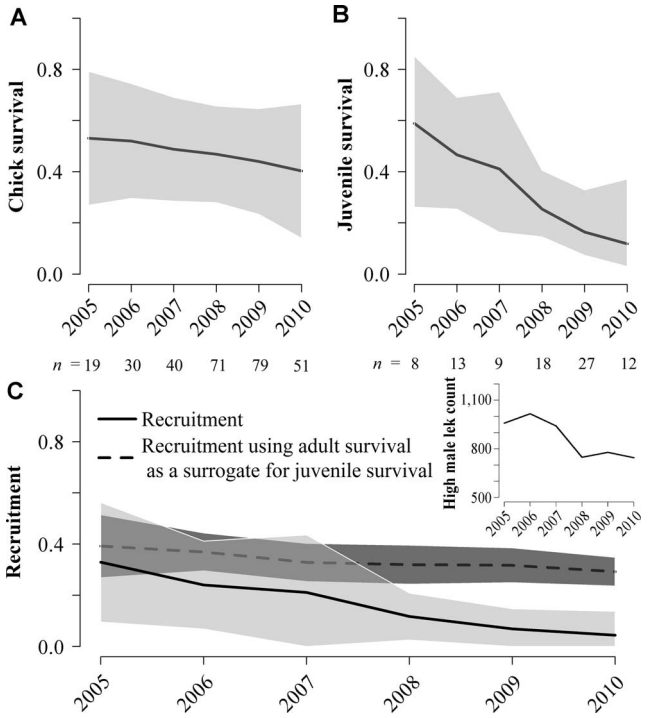


FIGURE 2. (**A**) Chick survival (0–30 days of age), (**B**) juvenile survival (31 days of age to March 31), and (**C**) recruitment (survival from hatching to incorporation into the first breeding season, March 31), with 95% confidence intervals, across years for Gunnison Sage-Grouse in the Gunnison Basin, Colorado, USA. Recruitment rates are shown as estimated from this study using chick and juvenile survival rates (solid line) and are compared with recruitment estimated using ASY (after-second-year) survival rates (Davis et al. 2015a) in lieu of juvenile survival (dashed lines). Corresponding high male lek counts in the Gunnison Basin are shown in the inset (U.S. Fish and Wildlife Service 2014).

confidence intervals were wide and the relationship was not definitive (Figure 2A).

The other factors included in the models (hen age and hatching week) were in ≤2 of the top models, and the year effect was in none of the top models. None of these factors had a cumulative w_i above 0.3 (Table 2), and therefore were not supported as being important factors for chick survival.

Juvenile Survival Analysis

The bootstrap analysis was run on the most parameterized model (16 parameters). There was weak evidence for overdispersion in the juvenile survival data ($\hat{c} = 1.103$); therefore, we did not use a $\hat{c}$ adjustment and models were compared using AIC_c.

The top model ($w_i = 0.534$; Table 3) included a trend effect and a season effect. Trend and season were the only factors that had a cumulative w_i above 0.50 (season = 0.998, and trend = 0.791; Table 2). Little support was evident for an effect of hatching week (cumulative w_i = 0.332), year-to-year variation (0.188), or monthly variability (0.002) on juvenile survival. As no chicks in the San Miguel population survived to 30 days of age, we were unable to estimate juvenile survival for this population.

Juvenile survival was lower and had larger variance during the summer and early fall (June to October), and was higher with less variance from November through March (Figure 3). Only 1 of the 87 birds included in the juvenile survival analysis died during the winter season (November–March), which corresponds to the narrow confidence intervals during this time frame (Figure 3). Among-year variability showed that juvenile survival declined from 2005 to 2010 (Figure 2B).

Recruitment Analysis

We based our recruitment estimates on the multiplication of the estimated chick and juvenile survival rates. Recruitment declined from 2005 to 2010 in the Gunnison Basin (Figure 2C, Table 4), and varied between 0.32 (95%

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

TABLE 3. Results of analysis of juvenile survival of Gunnison Sage-Grouse from the Gunnison Basin population, Colorado, USA, 2005–2010. Models were ranked by the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC_c). *K* is the number of parameters in the model, and w_i is the model weight.

Model [a]	ΔAIC_c	w_i	*K*	Deviance
Trend + Season	0.000 [b]	0.534	4	213.137
Trend + Season + Hatch	1.467	0.256	5	212.538
Season + Year	3.017	0.118	8	207.812
Year + Season + Hatch	4.084	0.069	9	206.760
Season	7.086	0.015	3	222.275
Season + Hatch	9.125	0.006	4	222.261
Trend + Month	12.581	0.001	11	210.975
Trend + Month + Hatch	14.110	0.000	12	210.342
Year + Month	15.901	0.000	15	205.561
Year + Month + Hatch	16.921	0.000	16	204.361
Month	17.742	0.000	10	218.284
Hatch + Month	19.820	0.000	11	218.214
Trend	35.362	0.000	2	252.589
Trend + Hatch	36.778	0.000	3	251.967
Year	39.468	0.000	6	248.461
Year + Hatch	40.352	0.000	7	247.252
Intercept only	45.588	0.000	1	264.841
Hatch	47.586	0.000	2	264.813

[a] 'Trend' represents a linear trend across years ($K = 1$); 'Season' denotes parameterization that allows monthly survival to vary by brood-rearing period (May–July), late summer and fall (August–October), and nonbreeding period (November–March; $K = 2$); 'Hatch' represents a linear trend based on the week in which the chick was hatched ($K = 1$); 'Year' denotes a separate parameter for each year in the study allowing for annual variability ($K = 6$); 'Month' denotes parameterization that allows for full monthly variability in survival ($K = 10$).
[b] The AIC_c value for the top model = 227.38.

CL = 0.15, 0.49) and 0.04 (95% CL = 0.00, 0.10). We also compared our estimated recruitment rates with recruitment rates calculated using chick survival and ASY survival estimates from Davis et al. (2015a). This comparison demonstrated that a critical trend would have been missed in recruitment over time if juvenile survival rates had not been monitored (Figure 2C).

DISCUSSION

One of the objectives of this study was to estimate and compare recruitment for 2 populations of Gunnison Sage-Grouse. The smaller population was limited in overall abundance (U.S. Fish and Wildlife Service 2014) and number of nests observed ($n = 20$), and had a low nest success rate (Davis et al. 2015b), thus resulting in a small sample of chicks included in our study ($n = 8$). None of these chicks survived to 30 days of age. Based on this small sample, we cannot calculate reliable estimates of chick survival for this population, as small samples sizes may give spurious results. However, during the same time

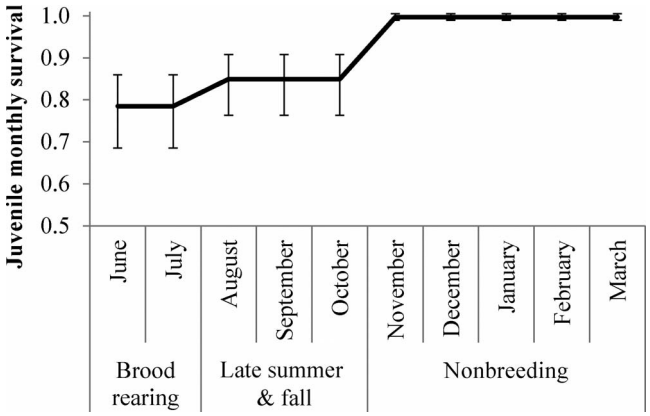


FIGURE 3. Within-year monthly survival rates, with standard errors, of juvenile Gunnison Sage-Grouse from the Gunnison Basin, Colorado, USA, 2005–2010.

frame, no SY individuals were captured in the San Miguel population (Davis et al. 2015a), supporting the idea that recruitment in this population is low. Another problem with small sample sizes is that they reduce the ability to detect differences even when true differences exist. Despite this, we did detect a difference in chick survival between our 2 study populations. Therefore, although the sample size from the San Miguel population was too small to robustly estimate chick survival, chick survival in the San Miguel population was likely lower than chick survival in the Gunnison Basin population. The rest of this discussion will focus on results from the Gunnison Basin population.

Chick and juvenile survival rates in the Gunnison Basin were similar to some rates that have been estimated for Greater Sage-Grouse (Aldridge 2005, Gregg and Crawford 2009, Swanson 2009). Although Greater Sage-Grouse chick survival rates are known to vary across years within a study (Walker 2008, Guttery et al. 2013) and across studies (Connelly et al. 2004, Taylor et al. 2012), chick survival rates in our study were relatively stable, with evidence of a weak decline across all years (Figure 2A). We did find strong evidence of a decline in juvenile survival rate estimates during our study in the Gunnison Basin (Figure 2B). There are many factors that may have

TABLE 4. Annual survival estimates (± standard errors) for the chick and juvenile stages and recruitment rates for Gunnison Sage-Grouse from 2005 to 2010 in the Gunnison Basin, Colorado, USA.

Year	Chick survival	Juvenile survival	Recruitment
2005	0.53 ± 0.13	0.62 ± 0.16	0.33 ± 0.12
2006	0.52 ± 0.11	0.46 ± 0.12	0.24 ± 0.09
2007	0.49 ± 0.10	0.43 ± 0.16	0.21 ± 0.11
2008	0.47 ± 0.10	0.25 ± 0.07	0.12 ± 0.05
2009	0.44 ± 0.11	0.16 ± 0.06	0.07 ± 0.04
2010	0.40 ± 0.13	0.11 ± 0.08	0.04 ± 0.05

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

contributed to the observed decline, including increased predation pressure and changes in habitat availability and quality. However, data were not available to test these hypotheses. ASY survival rates were stable over the same time interval (Davis et al. 2015a), suggesting that whatever was causing the decline in recruitment was influencing juveniles but not ASY birds. The last 3 years of the study saw the lowest recruitment rates, yet these years also had the highest nest success rates (Davis et al. 2015b). Caudill et al. (2014a) found a similar negative relationship between nest success and brood success, but with a 1 yr lag effect. Another possible explanation is that an abundance of chicks may lead to higher mortality rates in chicks and juveniles due to greater overall visibility and attractiveness to predators or increased intraspecific competition.

The Gunnison Basin population is considered to be a relatively stable population of Gunnison Sage-Grouse (Gunnison Sage-Grouse Rangewide Steering Committee 2005, U.S. Fish and Wildlife Service 2014). The decline in recruitment rate in the Gunnison Basin coincided with an estimated declining trend in the population based on index data (Figure 2C). This decline in population index values was not reflected in changes in ASY survival (Davis et al. 2015a), nest success rates (Davis et al. 2015b), or our observed chick survival rates. ASY survival, chick survival, and nest success all were identified as key demographic rates that influence growth rates for Greater Sage-Grouse (Taylor et al. 2012). We know that it is the interplay of vital rates that impacts population change; our study suggests that the juvenile survival rate and changes in that rate over time may also be an important contributor to population change in Gunnison Sage-Grouse. Population models for Gunnison Sage-Grouse demonstrate the strength of this demographic parameter on population growth (Davis 2012).

A decline in recruitment across time has been shown to be related to a general population decline in sage-grouse species (Connelly and Braun 1997, Gregg et al. 2007, Davis 2012). Previous research on galliforms has often concentrated on chick survival (Connelly and Braun 1997, Schroeder et al. 2004, Taylor et al. 2012), with comparatively few studies examining juvenile survival (Beck et al. 2006, Swanson 2009, Blomberg et al. 2014, Caudill et al. 2014b). Although chick survival is often logistically easier to study (based on the localized nature of early development and general reliance on parental care, where parents may be marked), our results highlight the importance of monitoring juvenile survival. The decline in Gunnison Sage-Grouse recruitment would have been masked had we only looked at chick survival (Figure 2C). These results highlight the fact that a gap in demographic information, such as a lack of species- or population-specific juvenile survival estimates, might skew population projections (e.g., Morris and Doak 2002).

We sought to evaluate the effect that sibling dependence had on survival rates. We found that a high level of sibling dependence occurred during the first 30 days of life, but that this dependence decayed as chicks became more independent as juveniles. Sibling dependence has also been observed in Greater Sage-Grouse chicks (Aldridge 2005, Guttery et al. 2013). When chicks in our study were captured for the first time, the majority had at least 1 sibling that was tagged ($n = 277/290$). Chicks during the first 30 days of life stay close to their mother, and therefore sibling proximity and behavior are inherently linked (Huwer 2004), which has led some research to focus on brood success instead of chick survival (Caudill et al. 2014a). Sage-Grouse young require protection against the elements at night through brooding by a hen, typically up to 60 days of age, and juvenile grouse tend to remain in flocks with their hen and siblings into the fall (Swanson 2009). However, there was little evidence for overdispersion in our juvenile survival analysis ($\hat{c} = 1.103$). The lack of overdispersion in our juvenile data may in part have been due to brood mixing, which occurs at a relatively high rate within sage-grouse (Connelly et al. 2006, Dahlgren et al. 2010, Thompson et al. 2015) and was observed in our study.

Sage-Grouse chick survival has been linked to many external effects; primary among them are factors relating to food and cover. Chick survival is generally better when there is greater forb cover (Drut et al. 1994b, Huwer 2004, Gregg and Crawford 2009), greater shrub and herbaceous cover (Aldridge 2005), and when arthropods are abundant (Drut et al. 1994b, Dahlgren et al. 2010). Drought conditions have been found to have a negative effect on chick survival (Aldridge 2005, Guttery et al. 2013). Although our study did not measure vegetation and arthropods at hen and brood locations, these associations might exist. Anecdotal evidence based on movement patterns of hens with chicks compared with hens without chicks suggests that forb and invertebrate availability are important for chicks, as hens with chicks seemed to spend more time in drainages and hay meadows with greener vegetation than hens without chicks.

We did not detect a difference in the success rate of chicks reared by SY vs. ASY birds. This is contrary to results from Greater Sage-Grouse research (Musil et al. 1993, Gregg et al. 2006). However, research on Greater Sage-Grouse suggests that the chicks of SY hens are more likely to leave their own brood than chicks of ASY hens, and that this likely enhances the survival rate of chicks with SY mothers (Dahlgren et al. 2010). Adoption occurred in our study; however, the rates of adoption were not well recorded and therefore we have no evidence to support this conjecture. However, if adoption rates do differ, this may help to explain why there was no discernable difference in survival of chicks hatched to SY vs. ASY hens.

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

We found that seasonal survival patterns within a year for Gunnison Sage-Grouse juveniles were similar to those for Greater Sage-Grouse juveniles (Blomberg et al. 2014, Caudill et al. 2014b), and that patterns also were similar for SY and ASY birds of both species (Davis et al. 2015a). The patterns found by Blomberg et al. (2014) were remarkably similar to our results, with lower survival in August to October–November and higher survival in the winter. However, our monthly survival estimates were slightly higher than those of Blomberg et al. (2014). Although the general patterns were similar, in that survival rates were lower in the summer and fall compared with the winter, juvenile survival rates during the summer and fall were considerably lower than those for SY and ASY birds during this same time period (Davis et al. 2015a; Figure 3). Survival rates in winter were high for juveniles, which more closely mimics results for ASY females than males. This survival pattern suggests that juveniles that survive until October will likely survive to the breeding season, which suggests that management efforts focused on juvenile survival during the summer months will likely be more efficient than working to improve fall and winter survival. Juvenile survival was lowest in the brood-rearing and late summer periods (June–October). During this period, sage-grouse are often found in meadows (Peterson 1970, Drut et al. 1994a) and riparian areas (Crawford et al. 2004, Dinkins et al. 2014) adjacent to sagebrush (Peterson 1970), particularly in areas with good grass and forb cover (Herman-Brunson 2007, Kirol et al. 2012). It may be beneficial to focus management on improving the quality and availability of these habitats and on increasing public awareness of the importance of these areas.

For threatened species, such as Gunnison Sage-Grouse, it is crucial that we understand the drivers of population change, as this understanding is necessary for targeting conservation efforts and for evaluating expected population longevity. Previous work has highlighted the importance of chick survival as a strong driver of population change for many bird species; however, our work has identified the need to extend monitoring to juvenile survival, as changes through time in juvenile survival rates may not be reflected in changes in other vital rates (chick survival, nest success, and SY or ASY survival). Additionally, we found differences in chick survival rates between 2 populations of Gunnison Sage-Grouse, which highlights the fact that management needs can be considerably different among populations. Johnson et al. (2010) emphasized the importance of managing populations according to their specific population dynamics and not assuming that the same management will be optimal across a species. The small, isolated San Miguel population represents unique genetic diversity for Gunnison Sage-Grouse (Oyler-McCance et al. 2005), which similarly has been found for isolated populations of Greater Sage-Grouse (Schulwitz et al. 2014, Davis et al. 2015c, Oyler-McCance et al. 2015). These genetic differences may be related to different processes exhibited by the different populations, and highlight the need to preserve the genetic diversity that is present in isolated populations. The lack of recruitment in the San Miguel population and the declining recruitment in the Gunnison Basin population are of concern for the fate of Gunnison Sage-Grouse, although longer-term views than that examined in this study do show promise that the trend that we observed is not continuing (Davis et al. 2014), and that this may be a downward swing in a cyclic process. It is essential that monitoring continues for the species, and future work should focus on the impacts of management actions to help improve conservation efforts for Gunnison Sage-Grouse.

ACKNOWLEDGMENTS

We thank Theresa Childers and Cameron Aldridge for their data collection efforts and all our field crews for their hard work. We especially thank Phillip Street for his dedication and commitment to this project. We are grateful to landowners in Gunnison, Saguache, and San Miguel counties in Colorado for their cooperation and support. Special thanks to Jim Gammonley and the staffs at the Gunnison Service Center (Area 16) and Montrose Service Center (Area 18) for logistic support and assistance with landowner contacts. Also, thanks to Gary White for assistance with Program MARK, to the Wagar 113 Superpopulation at Colorado State University, and to Eric Bergman, Reese Conrey, Susan Shriner, Eric Blomberg, and 2 anonymous reviewers for helpful reviews of previous drafts of this manuscript.

Funding statement: Funding for this project was provided by Colorado Parks and Wildlife, the National Parks Service, the U.S. Geological Survey, the U.S. Fish and Wildlife Service, and Colorado State University. None of the funders had any input into the content of the manuscript, nor required their approval of the manuscript prior to submission or publication.

Ethics statement: Field methods were approved by the Colorado Parks and Wildlife Animal Care and Use Committee (#02-2005). The study species was not federally protected during the course of the study.

Author contributions: A.J.D., M.L.P., and P.F.D. conceived the idea, design, and experiment (supervised research, formulated question or hypothesis); A.J.D. and M.L.P. performed the experiments (collected data, conducted the research); A.J.D., M.L.P., and P.F.D. wrote the paper (or substantially edited the paper); A.J.D., M.L.P., and P.F.D. developed or designed the methods; A.J.D. analyzed the data; and M.L.P. and P.F.D. contributed substantial materials, resources, or funding.

LITERATURE CITED

Aldridge, C. L. (2005). Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton, AB, Canada.

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

Anthony, R. G., and M. J. Willis (2009). Survival rates of female Greater Sage-Grouse in autumn and winter in southeastern Oregon. Journal of Wildlife Management 73:538–545.

Barbieri, M. M., and J. O. Berger (2004). Optimal predictive model selection. Annals of Statistics 32:870–897.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia (2006). Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Beck, T. D. I., R. B. Gill, and C. E. Braun (1975). Sex and age determination of Sage Grouse from wing characteristics. In Game Information Leaflet 49 (Revised), Colorado Division of Wildlife, Fort Collins, CO, USA.

Bishop, C. J., G. C. White, and P. M. Lukacs (2008). Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. Journal of Wildlife Management 72:1085–1093.

Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza (2014). Carryover effects and climatic conditions influence the postfledging survival of Greater Sage-Grouse. Ecology and Evolution 4:4488–4499.

Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese (2002). Attachment of radiotransmitters to one-day-old Sage Grouse chicks. Wildlife Society Bulletin 30:93–96.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Caudill, D., M. R. Guttery, B. Bibles, T. A. Messmer, G. Caudill, E. Leone, D. K. Dahlgren, and R. Chi (2014a). Effects of climatic variation and reproductive trade-offs vary by measure of reproductive effort in Greater Sage-Grouse. Ecosphere 5:1–11.

Caudill, D., T. A. Messmer, B. Bibles, and M. R. Guttery (2014b). Greater Sage-Grouse juvenile survival in Utah. Journal of Wildlife Management 78:808–817.

Connelly, J. W., and C. E. Braun (1997). Long-term changes in Sage Grouse (*Centrocercus urophasianus*) populations in western North America. Wildlife Biology 3:229–234.

Connelly, J. W., M. L. Commons-Kemner, J. L. Beck, K. P. Reese, E. O. Garton, N. A. Burkepile, and M. B. Lucia (2006). Sage-Grouse Ecology. Idaho Department of Fish and Game, Boise, ID, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver (2004). Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun (2000). Guidelines to manage Sage Grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd (2004). Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.

Dahlgren, D. K., T. A. Messmer, and D. N. Koons (2010). Achieving better estimates of Greater Sage-Grouse chick survival in Utah. Journal of Wildlife Management 74:1286–1294.

Davis, A. J. (2012). Gunnison Sage-Grouse demography and conservation. Ph.D. dissertation, Colorado State University. Fort Collins, CO, USA.

Davis, A. J., M. B. Hooten, M. L. Phillips, and P. F. Doherty, Jr. (2014). An integrated modeling approach to estimating Gunnison Sage-Grouse population dynamics: Combining index and demographic data. Ecology and Evolution 4:4247–4257.

Davis, A. J., M. L. Phillips, and P. F. Doherty, Jr. (2015a). Survival of Gunnison Sage-Grouse *Centrocercus minimus* in Colorado, USA. Journal of Avian Biology 46:186–192.

Davis, A. J., M. L. Phillips, and P. F. Doherty, Jr. (2015b). Nest success of Gunnison Sage-Grouse in Colorado, USA. PLOS One 10:e0136310. doi:10.1371/journal.pone.0136310

Davis, D. M., K. P. Reese, S. C. Gardner, and K. L. Bird (2015c). Genetic structure of Greater Sage-Grouse (*Centrocercus urophasianus*) in a declining, peripheral population. The Condor: Ornithological Applications 117:530–544.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey (2014). Greater Sage-Grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. The Condor: Ornithological Applications 116:629–642.

Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Doherty, P. F., Jr., G. C. White, and K. P. Burnham. (2012). Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Drut, M. S., J. A. Crawford, and M. A. Gregg (1994a). Brood habitat use by Sage Grouse in Oregon. Great Basin Naturalist 54:170–176.

Drut, M. S., W. H. Pyle, and J. A. Crawford (1994b). Diets and food selection of Sage Grouse chicks in Oregon. Journal of Range Management 47:90–93.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun (1982). Methods for trapping Sage Grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A., and J. A. Crawford (2009). Survival of Greater Sage-Grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

Gregg, M. A., M. R. Dunbar, and J. A. Crawford (2007). Use of implanted radiotransmitters to estimate survival of Greater Sage-Grouse chicks. Journal of Wildlife Management 71:646–651.

Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope (2006). Total plasma protein and renesting by Greater Sage-Grouse. Journal of Wildlife Management 70:472–478.

Gunnison Sage-Grouse Rangewide Steering Committee (2005). Gunnison Sage-Grouse Rangewide Conservation Plan. Colorado Division of Wildlife, Denver, CO, USA.

Guttery, M. R., D. K. Dahlgren, T. A. Messmer, J. W. Connelly, K. P. Reese, P. A. Terletzky, N. Burkepile, and D. N. Koons (2013). Effects of landscape-scale environmental variation on Greater Sage-Grouse chick survival. PLOS One 8:e65582. doi:10.1371/journal.pone.0065582

Hannon, S. J., and K. Martin (2006). Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology 269:422–433.

Heppell, S. S., H. Caswell, and L. B. Crowder (2000). Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Herman-Brunson, K. (2007). Nesting and brood-rearing habitat selection of Greater Sage-Grouse and associated survival of hens and broods at the edge of their historic distribution. M.S. thesis, South Dakota State University, Brookings, SD, USA.

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

Hupp, J. W., and C. E. Braun (1989). Topographic distribution of Sage Grouse foraging in winter. Journal of Wildlife Management 53:823–829.

Huwer, S. L. (2004). Evaluating Greater Sage-Grouse brood habitat using human-imprinted chicks. M.S. thesis, Colorado State University, Fort Collins, CO, USA.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen (2010). Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover (2012). Microhabitat selection for nesting and brood-rearing by the Greater Sage-Grouse in xeric big sagebrush. The Condor 114: 75–89.

Morris, W. F., and D. F. Doak (2002). Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, MA, USA.

Musil, D. D., J. W. Connelly, and K. P. Reese (1993). Movements, survival, and reproduction of Sage Grouse translocated into central Idaho. Journal of Wildlife Management 57:85–91.

Oyler-McCance, S. J., R. S. Cornman, K. L. Jones, and J. A. Fike (2015). Genomic single-nucleotide polymorphisms confirm that Gunnison and Greater sage-grouse are genetically well differentiated and that the Bi-State population is distinct. The Condor: Ornithological Applications 117:217–227.

Oyler-McCance, S. J., J. St. John, S. E. Taylor, A. D. Apa, and T. W. Quinn (2005). Population genetics of Gunnison Sage-Grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Peterson, J. G. (1970). The food habits and summer distribution of juvenile Sage Grouse in central Montana. Journal of Wildlife Management 34:147–155.

Pfister, C. A. (1998). Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences USA 95:213–218.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis (1989). Survival analysis in telemetry studies: The staggered entry design. Journal of Wildlife Management 53:7–15.

Powell, L. A. (2007). Approximating variance of demographic parameters using the delta method: A reference for avian biologists. The Condor 109:949–954.

Roff, D. A. (1992). Evolution of Life Histories. Prentice-Hall, New York, NY, USA.

Sæther, B.-E., and Ø. Bakke (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, et al. (2004). Distribution of sage-grouse in North America. The Condor 106:363–376.

Schulwitz, S., B. Bedrosian, and J. A. Johnson (2014). Low neutral genetic diversity in isolated Greater Sage-Grouse (*Centrocercus urophasianus*) populations in northwest Wyoming. The Condor: Ornithological Applications 116:560–573.

Seber, G. A. F. (1982). The Estimation of Animal Abundance and Related Parameters, second edition. Macmillan, New York, NY, USA.

Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson (2008). Polygyny and female breeding failure reduce effective population size in the lekking Gunnison Sage-Grouse. Biological Conservation 141:472–481.

Swanson, C. C. (2009). Ecology of Greater Sage-Grouse in the Dakotas. Ph.D. dissertation, South Dakota State University, Brookings, SD, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills (2012). Managing multiple vital rates to maximize Greater Sage-Grouse population growth. Journal of Wildlife Management 76:336–347.

Thompson, T. R., A. D. Apa, K. P. Reese, and K. M. Tadvick (2015). Captive rearing sage-grouse for augmentation of surrogate wild broods: Evidence for success. Journal of Wildlife Management 79:998–1013.

U.S. Fish and Wildlife Service (2014). Endangered and Threatened Wildlife and Plants; Threatened Status for Gunnison Sage-Grouse; Final Rule. Federal Register 79 FR 69191.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer (1992). An improved spotlighting technique for capturing Sage Grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L. (2008). Greater Sage-Grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. Ph.D. dissertation, University of Montana, Missoula, MT, USA.

White, G. C., and K. P. Burnham (1999). Program MARK: Survival Estimation from Populations of Marked Animals. Colorado State University, Fort Collins, CO, USA.

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

APPENDIX TABLE 5. Full table of model results for chick survival of Gunnison Sage-Grouse from the Gunnison Basin (2005–2010) and San Miguel (2007–2010) populations, Colorado, USA. The intercept-only model is shown for comparison. Models were ranked by the difference from the top model in Quasi–Akaike's Information Criterion ($\Delta QAIC_c$). K is the number of parameters in the model, and w_i is the model weight.

Model [a]	$\Delta QAIC_c$	w_i	K	QDeviance
Trend + Age + Population	0.000 [b]	0.139	4	444.232
Age + Population	0.186	0.127	3	446.422
Trend + Population	0.511	0.108	3	446.747
Population	0.632	0.101	2	448.870
Trend + Hatch + Age + Population	1.875	0.054	5	444.021
Age + Population + Hen age	1.952	0.052	4	446.184
Trend + Hen age + Age + Population	1.996	0.051	5	444.223
Age + Population + Hatch	2.183	0.047	4	446.416
Population + Hen age	2.395	0.042	3	446.557
Trend + Hatch + Population	2.404	0.042	4	448.630
Trend + Hen age + Population	2.510	0.040	4	446.742
Population + Hatch	2.622	0.037	3	448.866
Trend + Age + Population + Hatch + Hen age	3.879	0.020	6	444.020
Age + Population + Hatch + Hen age	3.957	0.019	5	446.154
Population + Hatch + Hen age	4.398	0.015	4	446.557
Trend + Hatch + Hen age + Population	4.408	0.015	5	448.606
Year + Age + Population	5.029	0.011	8	441.235
Year + Population	5.251	0.010	7	443.465
Trend + Age	5.375	0.009	3	451.610
Age	5.684	0.008	2	453.922
Year + Age + Population + Hatch	6.982	0.004	9	441.182
Year + Age + Population + Hen age	6.984	0.004	9	453.256
Age + Hen age	7.020	0.004	3	441.225
Year + Population + Hatch	7.188	0.004	8	443.420
Year + Population + Hen age	7.213	0.004	8	443.449
Trend	7.295	0.004	2	455.533
Trend + Hen age + Age	7.318	0.004	4	451.548
Trend + Hatch + Age	7.364	0.004	4	451.549
Intercept only	7.511	0.003	1	457.751
Age + Hatch	7.581	0.003	3	453.905
Hen age	8.817	0.002	2	457.055
Year + Age + Population + Hatch + Hen age	8.937	0.002	10	441.170
Age + Hatch + Hen age	9.003	0.002	4	453.255
Year + Population + Hatch + Hen age	9.151	0.001	9	443.403
Trend + Hen age	9.216	0.001	3	455.451
Trend + Hatch	9.292	0.001	3	451.470
Trend + Hatch + Hen age + Age	9.298	0.001	5	455.491
Hatch	9.378	0.001	2	457.724
Hatch + Hen age	10.785	0.001	3	457.055
Year + Age	11.158	0.001	7	449.373
Trend + Hatch + Hen age	11.207	0.001	4	455.391
Year	12.804	0.000	6	453.025
Year + Age + Hatch	13.142	0.000	8	449.372
Year + Age + Hen age	13.165	0.000	8	449.373
Year + Hatch	14.776	0.000	7	453.022
Year + Hen age	14.807	0.000	7	453.025
Year + Age + Hatch + Hen age	15.150	0.000	9	449.372
Year + Hatch + Hen age	16.781	0.000	8	453.021

[a] 'Trend' represents a linear trend across years ($K = 1$); 'Age' represents a linear trend on the age of the chick from 1 to 30 days of age ($K = 1$); 'Population' represents Gunnison Basin if it is a 0 and San Miguel if it is a 1 ($K = 1$); 'Hatch' represents a linear trend based on the week in which the chick was hatched ($K = 1$); 'Hen age' denotes the age of the hen: 0 for SY ($\leq$1 yr old) and 1 for ASY ($\geq$2 yr old; $K = 1$); 'Year' denotes a separate parameter for each year in the study allowing for annual variability ($K = 6$).

[b] The $QAIC_c$ value for the top model = 452.24.

Downloaded from https://academic.oup.com/condor/article/118/3/477/5153242 by guest on 23 January 2024

THE CONDOR
Ornithological Applications
www.cooper.org

Volume 116, 2014, pp. 629–642
DOI: 10.1650/CONDOR-13-163.1

RESEARCH ARTICLE

Greater Sage-Grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features

Jonathan B. Dinkins,[1]* Michael R. Conover,[1] Christopher P. Kirol,[2] Jeffrey L. Beck,[2] and Shandra Nicole Frey[1]

[1] Department of Wildland Resources, Utah State University, Logan, Utah, USA
[2] Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming, USA
* Corresponding author: jondinkins@hotmail.com

Submitted December 20, 2013; Accepted September 5, 2014; Published November 5, 2014

ABSTRACT

Prey species minimize the risk of predation directly by avoiding predators and indirectly by avoiding risky habitat. Habitat loss and fragmentation have been prevalent in Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") habitat, which has necessitated a better understanding of mechanisms driving habitat use. Using multinomial logistic regression, we compared landscape attributes and anthropogenic features (indirect mechanisms) and densities of avian predators (direct mechanisms) among 792 sage-grouse locations (340 nests, 331 early brood, and 121 late brood) and 660 random locations in Wyoming, USA, in 2008–2011. Anthropogenic features included oil and gas structures, communication towers, power lines, roads, and rural houses; and landscape attributes included a normalized difference vegetation index (NDVI), topographic ruggedness, the proportion of big sagebrush (*Artemisia* spp.), and proximity and proportion variables for forested and riparian habitats. Sage-grouse locations were best described with models that included multiple habitat variables and densities of small, medium, and large avian predators. Thus, both indirect and direct mechanisms of predator avoidance were employed by sage-grouse to select habitat and presumably lower their exposure to predation and nest predation. At all reproductive stages, sage-grouse selected flatter locations with a greater proportion of big sagebrush, a higher NDVI, and lower densities of oil and gas structures. Nest locations had a lower density of major roads and were farther away from riparian habitat; early-brood locations had a lower density of power lines and were closer to rural houses; and late-brood locations were closer to riparian habitat. The magnitudes of direct and indirect avoidance by sage-grouse hens were dependent on a sage-grouse's reproductive stage. Differential habitat use of female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest predation, while using habitat to meet their energetic requirements and those of their chicks.

Keywords: brood-site selection, corvid, habitat use, Greater Sage-Grouse, nest-site selection, predator avoidance, predation risk, raptor

Centrocercus urophasianus selecciona el hábitat basado en las aves depredadoras, la composición del paisaje y las características antropogénicas

RESUMEN

Las especies de presa minimizan el riesgo de depredación evitando directamente a los depredadores e indirectamente evitado los hábitats riesgosos. La pérdida de hábitat y la fragmentación han sido determinantes en el hábitat de *Centrocercus urophasianus*, lo que ha hecho necesaria una mejor comprensión de los mecanismos que determinan el uso del hábitat. Usando regresión logística multinomial, comparamos los atributos del paisaje y las características antropogénicas (mecanismos indirectos) y la densidad de aves depredadoras (mecanismos directos) entre 792 localizaciones de *C. urophasianus* (340 nidos, 331 crías recientes y 121 crías tardías) y 660 localizaciones al azar en Wyoming, entre 2008 y 2011. Las características antropogénicas incluyeron estructuras de petróleo y gas, torres de comunicación, tendidos eléctricos, caminos y casas rurales; y los atributos del paisaje incluyeron el índice normalizado de diferencia de vegetación (NDVI), rugosidad topográfica, proporción de especies de *Artemisia* y proximidad y proporción de hábitats boscosos y ribereños. Las localizaciones de *C. urophasianus* fueron mejor descritas con modelos que incluyeron múltiples variables de hábitat y densidad de aves predadoras pequeñas, medianas y grandes. Así, *C. urophasianus* usó mecanismos indirectos y directos de evasión de los depredadores para seleccionar los hábitats y bajar presumiblemente su exposición a la depredación y a la depredación de los nidos. En todos los estadios reproductivos, *C. urophasianus* seleccionó localizaciones más planas con una mayor proporción de especies de *Artemisia*, NDVI más elevado y densidades más bajas de estructuras de petróleo y gas. Las localizaciones de los nidos tuvieron menor densidad de caminos principales y estuvieron más alejadas de los hábitats ribereños; las localizaciones

© 2014 Cooper Ornithological Society. ISSN 0010-5422, electronic ISSN 1938-5129
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at aoucospubs@gmail.com

de las nidadas tuvieron menor densidad de tendidos eléctricos y estuvieron más cercanas a casa rurales; y las localizaciones de las nidadas tardías estuvieron más cerca a los hábitats ribereños. Las magnitudes de la evasión directa e indirecta por parte de los individuos de *C. urophasianus* dependieron del estadio reproductivo de *C. urophasianus*. Los diferentes usos de hábitat de las hembras de *C. urophasianus* con relación al riesgo de depredación y a la disponibilidad de alimentos fue aprovechada por los individuos de *C. urophasianus* para bajar su riesgo de depredación y la depredación de los nidos, durante el uso del hábitat para alcanzar los requerimientos energéticos de los adultos y los pichones.

Palabras clave: aves depredadores, *Centrocercus urophasianus*, córvido, evasión del depredador, rapaz, riesgo de depredación, selección de sitio de la nidada, selección de sitio del nido, uso de hábitat

INTRODUCTION

Predator avoidance behaviors influence habitat selection indirectly by reducing the use of risky habitats (habitats correlated with higher risk of predation) or directly by avoiding predators once they are seen (Lima 1998, Verdolin 2006, Cresswell 2008, Dinkins et al. 2012). Both indirect and direct mechanisms of predator avoidance are connected with an animal's perceived risk of predation (Cresswell 2008, Martin and Briskie 2009). For example, the risk of predation taken by male Red-breasted Nuthatches (*Sitta canadensis*) and White-breasted Nuthatches (*S. carolinensis*) to feed females on nests was lower in the presence of House Wrens (*Troglodytes aedon*) and Sharp-shinned Hawks (*Accipiter striatus*), which indicates direct avoidance of predators (Ghalambor and Martin 2000). Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") use habitat with lower densities of avian predators (Dinkins et al. 2012). Dinkins et al. (2012) suggested that the potential mechanism for this pattern was direct predator avoidance, but the pattern could also be explained in part as avoidance of habitat correlated with higher avian predator densities (e.g., oil and gas structures, power lines, forested habitat, etc.).

Anthropogenic features can be used as perches or nest structures by avian predators or can be associated with food subsides. American Kestrels (*Falco sparverius*; hereafter "kestrel"), Common Ravens (*Corvus corax*; hereafter "raven"), Golden Eagles (*Aquila chrysaetos*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*Buteo jamaicensis*), and Swainson's Hawks (*Buteo swainsoni*) use power lines for perching or nesting and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010, Coates et al. 2014, Howe et al. 2014). Road-killed animals also attract mammalian and avian predators (Bradley and Fagre 1988, Boarman 1993, Boarman et al. 1995, Frey and Conover 2006). Several studies have demonstrated that sagebrush-obligate birds, including Brewer's Sparrows (*Spizella breweri*), Sagebrush Sparrows (*Artemisiospiza nevadensis*), Vesper Sparrows (*Pooecetes gramineus*), and sage-grouse are negatively associated with oil and gas infrastructure (Aldridge 2005, Walker et al. 2007, Doherty 2008, Carpenter et al. 2010, Holloran et al. 2010, Gilbert and Chalfoun 2011). In addition, sage-grouse avoid power lines (Hanser et al. 2011) and roads (Holloran 2005, Aldridge and Boyce 2007). Thus, sagebrush birds, including sage-grouse, may avoid man-made features to indirectly reduce predation risk.

In addition to avoiding tall man-made structures (structures >2 m tall) and roads, prey species including sage-grouse may indirectly avoid avian predators by avoiding other landscape attributes that represent riskier habitat, such as riparian areas, coniferous forests, and rough terrain. In northeastern Wyoming, USA, Doherty et al. (2010) found that sage-grouse selected nesting habitat with lower terrain roughness and percent cover of conifer, grassland, and riparian habitat; they also found that sage-grouse selected areas with a greater density of sagebrush (*Artemisia* spp.) at the scale of 100 to 350 m compared with random locations within sagebrush. Greater density of sagebrush at relatively large spatial extents may reduce the foraging efficiency of visual predators. Reduced predation has the potential to increase not just sage-grouse adult survival but also nest success. For example, Brewer's Sparrows nesting in areas with greater shrub cover and a greater density of vacant potential nest sites had better nest success (Chalfoun and Martin 2009).

A better understanding of habitat quality and mechanisms driving habitat use is a key component of conservation of sage-grouse, a species of conservation concern (Braun 1998, Schroeder et al. 2004, Connelly et al. 2011). Little research has explicitly compared the relative importance of indirect vs. direct predator avoidance mechanisms in relation to the use of habitat by prey species, which could have implications for management recommendations. Sage-grouse may avoid avian predators indirectly by avoiding landscape attributes or anthropogenic features that might attract avian predators or directly by observing them; however, it is more likely that sage-grouse use both indirect and direct means of avoiding predators. We used sage-grouse as a model prey species to test the importance of both indirect and direct predator avoidance. From 2008 to 2011, we recorded avian predator densities and calculated distances from landscape attributes and anthropogenic features to radio-tagged sage-grouse hens to determine the importance of direct and indirect predator avoidance by sage-grouse hens. For

precocial species such as sage-grouse, predator avoidance may differ among reproductive stages (Ghalambor and Martin 2000). Thus, we also evaluated habitat use of sage-grouse females during two reproductive stages, nesting and brood-rearing. We hypothesized that sage-grouse primarily would avoid nesting and raising their chicks in areas with high densities of avian predators and secondarily would avoid landscape attributes and anthropogenic features that posed a greater risk of predation. We also hypothesized that sage-grouse hens would respond to multiple predator species by always avoiding avian predators, which are a threat to adult hen survival during all reproductive stages, but by avoiding predators that are threats to just nests and chicks only during those reproductive stages. Finally, we predicted that hens would use more productive, but riskier, riparian habitat only when chicks were less vulnerable to predation.

METHODS

Study Area

Our study was conducted at 12 sites in southwestern and south-central Wyoming, USA. Holloran and Anderson (2005) found that 93% of 415 observed nests were within 8.5 km of leks at which females were captured in central and southwestern Wyoming. Thus, our eight sites in southwestern Wyoming (Lincoln, Sweetwater, and Uinta counties) were 16 km in diameter, approximately centered around leks where hens were captured. The four sites in south-central Wyoming (Carbon and Sweetwater counties) were 24 km in diameter, because sage-grouse were captured at several nearby leks over a larger area. Sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming, with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,600 m. Most of the area within our sites was federally owned and administered by the Bureau of Land Management, with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in our sites. All sites had anthropogenic development, which consisted mostly of unimproved four-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of our sites; mean well density among all sites was 0.12 ± 0.22 SD wells km^{-2} (minimum–maximum = 0.00–0.64 wells km^{-2}).

The landscape at all sites was dominated by sagebrush; Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and little sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides.

Sage-grouse Capture and Monitoring

We monitored sage-grouse hens during nesting and brood-rearing from 2008 to 2011. Hens were captured, radio-tagged, and released in April of each year. We captured hens at night using all-terrain vehicles (ATVs), spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g ($<$1.5% body mass) necklace radio-collars (RI-2D, Holohil Systems, Carp, Ontario, Canada; or A4060, Advanced Telemetry Systems, Isanti, Minnesota, USA).

We located hens weekly with Communications Specialists receivers (R-1000, Communications Specialists, Orange, California, USA) and three-way Yagi antennas. Potential nests were identified with binoculars from $\sim$15 m away by visually locating a radio-tagged hen under a shrub. Nests were verified by triangulating the hen under the same shrub from $>$50 m away or thoroughly searching the area of the potential nest when the hen was absent. We continued monitoring nests weekly until the nest hatched or failed.

We located the broods of radio-tagged hens weekly with binoculars from $\sim$15 m distance. Brood hens were identified either by visually detecting chicks or by observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, clucking). If there was evidence of at least one chick with a sage-grouse hen, we classified the hen as early brood (chicks $<$4 weeks of age) or late brood (chicks 4–8 weeks of age). Monitoring of broods continued for as long as possible, which was usually until the chicks were 3–8 weeks posthatch, the hen lost her brood, the hen died, or the hen could no longer be located.

Avian Predator Monitoring

To quantify avian predators, we used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all avian predators observed during point counts and recording their distance from the observer. Point counts were conducted at random and sage-grouse (nest, early brood, and late brood) locations. Random locations were selected from habitat dominated by sagebrush within 8 km of the leks where sage-grouse were captured. This was intended to quantify avian predator density in habitat available for use by sage-grouse (Dinkins et al. 2012). Within each year, random locations were $>$2,000 m apart.

Point counts at sage-grouse nests were established when hens had begun incubating; thus, we assumed that we detected raptors and corvids that were present when nests were initiated. For a detailed description of point count methods see Dinkins et al. (2012) and Dinkins (2013). All avian predator variables were calculated from the raw count data within effective detection radii (EDR) estimated with DISTANCE version 6.0 release 2 (Thomas et al. 2010), as specified in Dinkins et al. (2012). Thus, *Buteo* spp. hawk, Golden Eagle, Northern Harrier (*Circus cyaneus*; hereafter "harrier"), kestrel, Black-billed Magpie (*Pica hudsonia*; hereafter "magpie"), and raven densities were individually calculated within 450 m, 1,000 m, 350 m, 400 m, 300 m, and 600 m, respectively, of each point count location (see Dinkins et al. 2012 for further details). We did not include other falcons or owls because they were rarely detected during point counts. Raw densities were standardized by the number of visits to each point count location and were log-transformed.

Anthropogenic and Landscape Feature Variables

We used ArcMap 10.0 (Esri, Redlands, California, USA) to calculate point count proximity (Euclidean distance) to anthropogenic features that could be used as perch or nest sites by avian predators or could provide food subsidies. We quantified the distance from each point count location to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy-extraction-related building), major road, any road type, communication tower, house, or power line. Densities of anthropogenic structures were calculated at four spatial extents (0.27-km, 0.54-km, 1.00-km, and 3.00-km radii) for oil and gas structures (number km^{-2}), major roads (km km^{-2}), all road types (km km^{-2}), houses (number km^{-2}), and power lines (km km^{-2}). The four spatial extents were derived from previous research on sage-grouse (Holloran and Anderson 2005, Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2010, Aldridge et al. 2011, Hanser et al. 2011). Ongoing energy development was occurring in half of our sites, which required us to assess the dates that energy-related structures and roads were added or removed from the landscape.

In distance calculations, we included only oil and gas structures and roads that existed when each point count was conducted. We obtained information on oil and gas structures, including the date that construction started on the structure and the date when wells were plugged and abandoned (the date that the structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; http://wogcc.state.wy.us). We verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture 2010). Aerial imagery from NAIP is produced by the U.S. Department of Agriculture (USDA) on a 3-yr rotation; thus, we used WOGCC data and on-the-ground GPS units to map energy development that occurred after August 2009.

We used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved roads, improved gravel roads, and railroads; all roads included major roads and all unimproved four-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power-line mapping.

Sage-grouse were likely to respond to many different types of anthropogenic structure in a similar manner (e.g., select locations farther away from all tall structures). Thus, we created two anthropogenic structure variables that represented the nearest: (1) distance to an oil and gas structure, communication tower, or house (WCH); and (2) distance to an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from point count locations to individual types of anthropogenic structures.

Similarly to anthropogenic feature calculations, we used ArcMap 10.0 to calculate the distance from every point count location to landscape attributes including forested (deciduous or coniferous stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data (http://gap.uidaho.edu/index.php/nw-gap/land-cover) from 2011, and verified with NAIP imagery from 2009. At our sites, riparian habitat from ReGAP consisted of mesic areas with patchy shrubs. In addition to distance variables, we calculated a normalized difference vegetation index (NDVI) and the proportion of forested, riparian, and big sagebrush habitats around all point count locations. We extracted NDVI values that were generated by Aldridge et al. (2011) and Hanser et al. (2011) for the Wyoming Basins Ecoregion, which were created from 250 m MODIS (Moderate Resolution Imaging Spectroradiometer) satellite imagery (http://modis.gsfc.nasa.gov/) between May and August of 2004. These NDVI values represent relative NDVI among point count locations during the sage-grouse nesting and brood-rearing season. Topography with greater surface roughness had the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that could provide vantage points for avian predators. Riley et al. (1999) created a topographic ruggedness index (TRI) to describe the roughness of landscapes, quantified as the difference in elevation among adjacent pixels of a digital

elevation map averaged over a user-defined area. For every point count location, we used ArcMap 10.0 to extract TRI values generated by Aldridge et al. (2011) and Hanser et al. (2011). Proportion of habitat (big sagebrush, forested, and riparian), NDVI, and TRI variables were constructed at four spatial extents (0.23-km^2, 0.92-km^2, 3.14-km^2, and 28.26-km^2) by using a moving window analysis within 0.27-km, 0.54-km, 1.00-km, and 3.00-km radii, respectively (Aldridge et al. 2011, Hanser et al. 2011).

Euclidean distance is not a good measure of habitat selection by wildlife, because the response of a species to landscape attributes or anthropogenic features often declines as distance increases (Carpenter et al. 2010, Aldridge et al. 2011, Fedy and Martin 2011, Hanser et al. 2011). Thus, we calculated distance decay functions to allow for nonlinear avoidance of landscape attributes or anthropogenic features, expressed as:

$$\text{Decay function} = \exp^{(\text{Euclidean distance to feature(km)}/-\text{decay distance})}.$$

We calculated all decay functions with three decay distances (0.25 km, 0.50 km, and 1.00 km). The value of the 0.25-, 0.50-, and 1.00-km decay functions approached 0 at ~1.2, ~2.4, and ~4.5 km, respectively. The distance at which decay function values approached 0 approximated the home range size of Golden Eagles and ravens (Boarman and Heinrich 1999, DeLong 2004). Decay functions scaled distance variables between 0 and 1, with greater values corresponding to point count locations closer to landscape attributes or anthropogenic features.

Data Analyses

We fit multinomial logistic regression models with maximum likelihood using function multinom in package nnet version 7.3–4 in R (R 2.14.2; R Development Core Team 2012) to evaluate habitat selection of nesting and brood-rearing sage-grouse hens. In addition to our full analysis, we conducted the same analysis with the exclusion of anthropogenic features on a subset of random and sage-grouse locations that were at least 3 km away from oil and gas structures, communication towers, power lines, rural houses, and major roads. This analysis was intended to verify whether sage-grouse response to avian predators was consistent regardless of influences from anthropogenic structures. Multinomial logistic regression models have been used to model habitat selection of wildlife species with >2 response categories (McCracken et al. 1998, McDonald et al. 2006, Bañuelos et al. 2008). We categorized point count locations into four response categories: (1) random, (2) sage-grouse nest, (3) early brood, and (4) late brood. Random point counts were kept in a single category across the summer, because we did not detect differences in avian densities between the first and second half of summer (Dinkins 2013); thus, modeling with multinomial logistic regression was more efficient as we could compare all response categories simultaneously rather than having to conduct a series of binomial regressions. Multinomial logistic regression uses one category as the reference for comparisons with all other categories; thus, each analysis can directly compare all categories among themselves by iteratively changing the reference category in the same model. To compare sage-grouse habitat selection with available sagebrush habitat (random locations), we made comparisons of sage-grouse locations with random locations by coding random locations as the reference category. We then alternated nest and early-brood location as the reference category to directly compare among sage-grouse locations.

Modeling of sage-grouse habitat selection was conducted using an information-theoretic approach (Anderson 2008). We compared models with Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002) using function aictab in package AICcmodavg version 1.25 in R (Mazerolle 2012). We employed sequential AIC_c modeling of covariate sets (anthropogenic, landscape, and avian predator), which Arnold (2010) suggested as an appropriate approach for identifying and ranking the most parsimonious models. Noninformative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC_c-selected models among covariate sets (Arnold 2010). We classified models within 2 AIC_c of the null model as being noncompetitive (Burnham and Anderson 2002); thus, any model within 2 AIC_c of the null was omitted from further analyses.

The best spatial extent and functional form of variables describing the effects of landscape attributes and anthropogenic features on habitat selection by sage-grouse were determined through AIC_c prior to sequential modeling of covariate sets (Step 1). We did not include WCH or ANTH with any anthropogenic structure variable that was used to create WCH or ANTH. For all distance decay functions, we chose the best decay distance (0.25 km, 0.50 km, and 1.00 km) for each distance variable by comparing AIC_c values. We compared models with individual density, proportion, and TRI variables measured at 0.27-km, 0.54-km, 1.00-km, and 3.00-km radii using AIC_c to choose the best spatial extent for each of those variable groups to be used in the anthropogenic and landscape covariate sets. Density and proportion variables were compared to the analogous proximity variables with AIC_c, and the best functional form of each variable was used in all further modeling (Table 1).

In Step 2, anthropogenic and landscape covariate sets were evaluated sequentially to identify the variables to be included in the best models for each of those covariate sets

TABLE 1. Variables selected in Step 1 of our modeling process and used in analysis of habitat selection by sage-grouse hens at nest ($n = 340$), early-brood ($n = 331$), and late-brood ($n = 121$) locations at 12 sites in southern Wyoming, USA, 2008–2011. Subscripts indicate best spatial extent or distance decay (km), and descriptions indicate best functional form (see Results).

Covariate set and variable name	Variable description
Anthropogenic	
$OGSden_{3.0}$	Density of oil and gas structures (energy wells, compressor stations, transfer stations, refineries, and other energy extraction related buildings; no. km^{-2})
$POWden_{3.0}$	Density of power lines (km km^{-2})
$MRDden_{3.0}$	Density of major roads (km km^{-2})
$HOM_{1.0}$	Distance decay function to nearest rural house
$WCHden_{1.0}$	Density of oil and gas structures, communication towers, and houses (no. km^{-2})
$ANTH_{0.25}$	Distance decay function to nearest oil and gas structure, communication tower, house, or power line
Landscape	
$SAGEpro_{1.0}$	Proportion of big sagebrush (*Artemisia* spp.) landcover
$TREE_{0.25}$	Distance decay function to nearest forested habitat including deciduous and coniferous stands
$RIP_{1.0}$	Distance decay function to nearest riparian habitat
$TRI_{0.54}$	Topographic ruggedness index
$NDVI_{0.27}$	Normalized difference vegetation index
Avian predator	
Small avian predators	Aggregated density of Black-billed Magpies and American Kestrels calculated from raw point counts within species-specific effective detection radii (300 m and 400 m, respectively)
Medium avian predators	Aggregated density of Common Ravens, *Buteo* hawks, and Northern Harriers calculated from raw point counts within species-specific effective detection radii (600 m, 450 m, and 350 m, respectively)
Large avian predators	Density of Golden Eagles calculated from raw point counts within the species-specific effective detection radius of 1,000 m

(i.e. models within 2 AIC_c of the top model within each covariate set). As the final modeling step (Step 3), we compared all top AIC_c-selected models from anthropogenic and landscape covariate sets and the best avian predator model from Dinkins et al. (2012) among each other and as additive models. The avian predator model included three avian predator variables (small, medium, and large avian predators), and three of the four years of data were from Dinkins et al. (2012). The three avian predator variables were constructed by aggregating raw avian predator densities calculated within species-specific EDRs based on the size of the avian predator, which resulted in small (magpie and kestrel), medium (*Buteo* hawk, harrier, and raven), and large (Golden Eagle) avian predator variables. This avian predator model was shown by Dinkins et al. (2012) to describe potential sage-grouse avoidance of avian predators better than models based on: individual species; distinguishing among different avian predator foraging styles; or avian predator threat to sage-grouse hens, nests, or broods. We based our inference on models within 2 AIC_c of the top selected model (Burnham and Anderson 2002). We prevented multicollinearity by not including in any model any two variables that covaried ($r > 0.65$) as determined with a Pearson's correlation matrix; thus, we eliminated one covarying variable from further analysis by retaining the variable that made the most biological sense.

Although we could not test for spatial autocorrelation in multinomial logistic regressions, avian predator densities derived from distance-sampling techniques were robust to lack of independence of observation locations because distance sampling was set up to be a snapshot in time (Thomas et al. 2010). Our avian predator sampling was designed to count the greatest proportion of the actual number of avian predators within a site each week while not counting the same avian predator more than once per week, as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual avian predator during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. We replicated point counts in multiple weeks to increase detection of avian predators (Thomas et al. 2010). When evaluating avian predator densities between sage-grouse and random locations, Dinkins et al. (2012) accounted for spatial autocorrelation in generalized linear mixed models; however, accounting for spatial autocorrelation did not significantly change the coefficient values of their avian predator models. Furthermore, multinomial logistic regression only requires that successive habitat selection choices be independent (Agresti 2007).

TABLE 2. Multinomial logistic regression models comparing landscape-attribute and anthropogenic-feature variables as covariate sets among locations used by sage-grouse (nest: $n = 340$, early-brood: $n = 331$, and late-brood: $n = 121$ locations) and random locations ($n = 660$) at 12 sites in southern Wyoming, USA, 2008–2011. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight. See Table 1 for variable descriptions.

Model	K	ΔAIC_c	w_i	Deviance
Anthropogenic covariate set				
$OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$ [a]	15	0.00	0.98	3522.16
$OGSden_{3.0}$, $POWden_{3.0}$, $HOM_{1.0}$	12	8.02	0.02	3536.30
$OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$	12	17.17	0.00	3545.44
$OGSden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$	12	19.84	0.00	3548.12
$OGSden_{3.0}$, $POWden_{3.0}$	9	20.62	0.00	3555.00
$POWden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$	12	22.22	0.00	3550.50
$POWden_{3.0}$, $HOM_{1.0}$	9	27.69	0.00	3562.06
$OGSden_{3.0}$, $MRDden_{3.0}$	9	34.02	0.00	3568.38
$POWden_{3.0}$, $MRDden_{3.0}$	9	40.72	0.00	3575.08
$POWden_{3.0}$	6	42.27	0.00	3582.70
Landscape covariate set				
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$ [b]	15	0.00	0.80	3432.84
$SAGEpro_{1.0}$, $TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	18	2.80	0.20	3429.50
$SAGEpro_{1.0}$, $TREE_{0.25}$, $RIP_{1.0}$, $NDVI_{0.27}$	15	16.19	0.00	3449.02
$SAGEpro_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	19.05	0.00	3458.00
$SAGEpro_{1.0}$, $TREE_{0.25}$, $TRI_{0.54}$, $NDVI_{0.27}$	15	23.25	0.00	3456.10
$SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$	12	27.12	0.00	3466.08
$SAGEpro_{1.0}$, $TREE_{0.25}$, $NDVI_{0.27}$	12	37.21	0.00	3476.16
$TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	15	38.59	0.00	3471.42
$RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	39.71	0.00	3478.66
$SAGEpro_{1.0}$, $NDVI_{0.27}$	9	44.24	0.00	3489.30

[a] $AIC_c = 3552.49$.
[b] $AIC_c = 3463.17$.

RESULTS

Avian Predators, Landscape Attributes, and Anthropogenic Features Analysis

We conducted 4,441 point count surveys at 1,452 locations during 2008–2011, including 340 sage-grouse nest, 331 sage-grouse early-brood, 121 sage-grouse late-brood, and 660 random locations. These locations were compiled from 289 hens with a mean of 1.2 nests per hen, 2.9 early-brood locations per hen, and 3.0 late-brood locations per hen. Brood locations were compiled from 124 separate sage-grouse broods from 114 sage-grouse hens. We counted 196 *Buteo* hawks, 295 Golden Eagles, 77 harriers, 105 kestrels, 143 magpies, and 688 ravens within species-specific EDRs (Dinkins et al. 2012), which equated to 248 small, 961 medium, and 295 large avian predators. These counts do not necessarily indicate unique individuals, but rather detections used to quantify density around localized areas. Brood, nest, and random locations aggregated across all years were on average 598.0 m (38.8 m SE), 908.6 m (9.6 m SE), and 1,189 m (25.5 m SE) apart, respectively. Avian predator variables did not covary with any other variables ($r^2 < 0.02$, variance inflation factor [VIF] ≤ 2.2), indicating no multicollinearity between avian predator variables and anthropogenic or landscape feature variables.

During Step 1, our modeling generally suggested that anthropogenic features were influencing sage-grouse habitat selection at a larger spatial extent (3-km radius) than were landscape attributes (<1-km radius; Table 1). The best spatial extent for density variables was within 3 km of a point count location. Densities of oil and gas structures ($OGSden_{3.0}$), power lines ($POWden_{3.0}$), and major roads ($MRDden_{3.0}$) fit the data better than raw distance or distance decay functions. The best spatial extents for the proportion of big sagebrush ($SAGEpro_{1.0}$), TRI ($TRI_{0.54}$), and NDVI ($NDVI_{0.27}$) were within 1.00 km, 0.54 km, and 0.27 km, respectively. Distance to rural houses ($HOM_{1.0}$) and riparian habitat ($RIP_{1.0}$) as 1-km distance decay functions fit the data better than Euclidean distance or densities. The effects of $HOM_{1.0}$ and $RIP_{1.0}$ on sage-grouse selection of nesting and brood locations became negligible beyond approximately 4 km (i.e. 1 km distance decay approaches zero at approximately 4 km away from an object of interest).

During Step 2 of sequential modeling, we found that sage-grouse selection of nest and brood locations was partially based on landscape attributes and anthropogenic features (Table 2). The top AIC_c-selected anthropogenic feature model ($w_i = 0.98$) included $OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$, and $HOM_{1.0}$ (Table 2). The top AIC_c-selected

TABLE 3. Multinomial logistic regression models comparing anthropogenic and landscape covariate sets (top models from Table 2) and the avian predator model (including small, medium, and large avian predator densities) among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations at 12 sites in southern Wyoming, USA, 2008–2011. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight.

Model	K	ΔAIC_c	w_i	Deviance
Avian, anthropogenic, landscape [a]	36	0.00	1.00	3042.14
Avian, landscape	24	38.24	0.00	3105.42
Avian, anthropogenic	24	141.46	0.00	3208.62
Avian	12	203.45	0.00	3295.24
Anthropogenic, landscape	27	295.98	0.00	3356.92
Landscape	15	347.16	0.00	3432.84
Anthropogenic	15	436.48	0.00	3522.16
Intercept only	3	509.13	0.00	3619.12

[a] $AIC_c = 3116.01$.

landscape feature model ($w_i = 0.80$) included $SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$, and $TRI_{0.54}$ (Table 2). During Step 3 of sequential modeling, our analyses indicated that sage-grouse hen selection of nest and brood locations was best described by small, medium, and large avian predator densities (avian predator model) in conjunction with many landscape attributes and anthropogenic features ($w_i = 1.00$; Table 3). This indicates that sage-grouse respond to multiple factors related to habitat quality, including factors related to perceived predation risk (landscape attributes and anthropogenic features) and direct predation risk (avian predator densities).

Greater densities of small, medium, and large avian predators were negatively correlated with sage-grouse nest, early-brood, and late-brood locations compared with random locations (Table 4). Early-brood and late-brood sage-grouse locations had lower avian predator densities than nesting sage-grouse locations (Table 5). Within each reproductive stage, sage-grouse locations had similar negative coefficient values for small and medium avian predators, but exhibited greater negative coefficient values for large avian predators (Golden Eagles) compared with small and medium avian predators (Tables 4 and 5).

In general, sage-grouse responded to most anthropogenic features by avoiding them, regardless of the sage-grouse's reproductive stage; however, many of these effects had parameter estimates with 95% CI that overlapped zero for all reproductive stages (Tables 4 and 5). In contrast to the avoidance of other anthropogenic structures, our analyses indicated that early-brood and late-brood sage-grouse were closer to rural houses ($HOM_{1.0}$ parameter estimate was positive) compared with random locations and nest locations (Tables 4 and 5). We found that nesting, early-brood, and late-brood sage-grouse were in areas with lower $OGSden_{3.0}$ compared with random locations (Table 4). However, the effect of $OGSden_{3.0}$ on sage-grouse habitat use during nesting had a parameter estimate with 95% CI that overlapped zero (Table 4). Sage-grouse use of habitat was negatively associated with $MRDden_{3.0}$ during all reproductive stages, with 95% CI of parameter estimates overlapping zero for brood locations (Table 4). Early-brood and late-brood sage-grouse locations had lower $POWden_{3.0}$ compared with random locations (Table 4).

For landscape attribute variables, we found that sage-grouse differed in their response to proximity to riparian habitat ($RIP_{1.0}$) depending on their reproductive stage. Compared with random locations, sage-grouse selected nest locations farther away from riparian habitat ($RIP_{1.0}$ parameter estimate was negative), but early-brood sage-grouse neither selected nor avoided habitat based on

TABLE 4. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 2 and 3). This analysis compares either nest, early-brood, or late-brood locations used by sage-grouse with random (reference category) locations at 12 sites in southern Wyoming, USA, 2008–2011. See Table 1 for variable descriptions.

	Nest vs. random			Early-brood vs. random			Late-brood vs. random		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−7.83 (0.91)	−9.61	−6.05*	−17.57 (1.51)	−20.54	−14.60*	−18.25 (1.98)	−22.14	−14.35*
Small avian predator	−0.09 (0.03)	−0.15	−0.02*	−0.34 (0.06)	−0.47	−0.21*	−0.33 (0.09)	−0.52	−0.16*
Medium avian predator	−0.08 (0.02)	−0.12	−0.04*	−0.28 (0.03)	−0.34	−0.21*	−0.28 (0.05)	−0.38	−0.19*
Large avian predator	−0.14 (0.05)	−0.23	−0.05*	−0.59 (0.12)	−0.82	−0.36*	−0.45 (0.14)	−0.73	−0.19*
$OGSden_{3.0}$	−0.37 (0.20)	−0.75	0.02	−0.56 (0.24)	−1.03	−0.09*	−3.18 (1.01)	−5.16	−1.20*
$POWden_{3.0}$	0.44 (0.67)	−0.88	1.76	−2.52 (0.97)	−4.44	−0.61*	−5.28 (1.71)	−8.64	−1.92*
$HOM_{1.0}$	0.12 (0.84)	−1.53	1.76	2.16 (0.79)	0.59	3.73*	2.56 (0.99)	0.62	4.50*
$MRDden_{3.0}$	−2.99 (1.31)	−5.58	−0.41*	−1.52 (1.48)	−4.44	1.40	−2.00 (2.54)	−7.01	3.02
$SAGEpro_{1.0}$	3.42 (0.58)	2.28	4.55*	2.17 (0.59)	1.02	3.33*	1.21 (0.78)	−0.32	2.75
$RIP_{1.0}$	−0.86 (0.28)	−1.42	−0.31*	−0.26 (0.29)	−0.83	0.31	0.85 (0.40)	0.05	1.64*
$TRI_{0.54}$	−0.04 (0.01)	−0.05	−0.02*	−0.02 (0.01)	−0.03	−0.01*	0.02 (0.01)	−0.04	<0.00*
$NDVI_{0.27}$	6.72 (1.06)	4.62	8.81*	5.97 (1.11)	3.78	8.16*	9.00 (1.36)	6.32	11.68*

* Denotes a 95% confidence interval that does not include zero.

TABLE 5. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 2 and 3). The reference category was alternated from random to nest or early-brood location to facilitate direct comparison of locations used by sage-grouse at 12 sites in southern Wyoming, USA, 2008–2011. See Table 1 for variable descriptions.

	Early-brood vs. nest [a]			Late-brood vs. nest [a]			Late-brood vs. early-brood [b]		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−9.74 (1.56)	−12.82	−6.66*	−10.42 (2.01)	−14.38	−6.45*	−0.68 (2.27)	−5.15	3.79*
Small avian predator	−0.26 (0.07)	−0.39	−0.13*	−0.25 (0.09)	−0.42	−0.07*	0.01 (0.10)	−0.20	0.21
Medium avian predator	−0.20 (0.03)	−0.27	−0.13*	−0.21 (0.05)	−0.30	−0.11*	0.00 (0.05)	−0.11	0.10
Large avian predator	−0.45 (0.12)	−0.69	−0.22*	−0.32 (0.14)	−0.60	−0.04*	0.14 (0.18)	−0.21	0.49
$OGSden_{3.0}$	−0.19 (0.27)	−0.72	0.33	−2.82 (1.01)	−4.81	−0.82*	−2.62 (1.01)	−4.61	−0.63*
$POWden_{3.0}$	−2.97 (1.01)	−4.94	−0.98*	−5.73 (1.72)	−9.11	−2.34*	−2.76 (1.76)	−6.22	0.70
$HOM_{1.0}$	2.04 (0.88)	0.32	3.78*	2.44 (1.05)	0.37	4.52*	0.40 (0.88)	−1.34	2.14
$MRDden_{3.0}$	1.47 (1.71)	−1.89	4.83	0.99 (2.68)	−4.28	6.27	−0.48 (2.62)	−5.64	4.68
$SAGEpro_{1.0}$	−1.24 (0.66)	−2.54	0.05	−2.20 (0.83)	−3.85	−0.56*	−0.96 (0.80)	−2.54	0.62
$RIP_{1.0}$	0.60 (0.32)	0.03	1.23	1.71 (0.43)	0.87	2.54*	1.11 (0.41)	0.30	1.91*
$TRI_{0.54}$	0.02 (0.01)	0.00	0.04*	0.02 (0.01)	0.00	0.04*	0.00 (0.01)	−0.02	0.02
$NDVI_{0.27}$	−0.75 (1.12)	−2.97	1.47	2.28 (1.36)	−0.41	4.97	3.03 (1.29)	0.48	5.58*

* Denotes a 95% confidence interval that does not include zero.
[a] Nest as reference category. This analysis also included random locations; however, those results are in Table 4.
[b] Early-brood as reference category. This analysis also included random and nest locations; however, those results are in the early-brood vs. nest and late-brood vs. nest columns and Table 4.

proximity to riparian habitat, and late-brood sage-grouse selected locations closer to riparian habitat ($RIP_{1.0}$ parameter estimate was positive; Table 4). However, both early-brood and late-brood locations were closer to riparian habitat compared with nest locations ($RIP_{1.0}$ parameter estimate was positive), and late-brood locations were closer to riparian habitat than early-brood locations ($RIP_{1.0}$ parameter estimate was positive; Table 5). $SAGEpro_{1.0}$ was positively associated with sage-grouse locations during nesting and early brood rearing (Table 4). $NDVI_{0.27}$ was positively associated with sage-grouse locations at all reproductive stages (Table 4). Sage-grouse during all reproductive stages were located in areas with flatter topography ($TRI_{0.54}$ parameter estimates were negative) compared with random locations (Table 4).

Avian Predators and Landscape Attributes Analysis

Our analysis that excluded locations within 3 km of anthropogenic structures comprised 2,406 point count surveys at 803 locations during 2008–2011. This equated to 153 sage-grouse nest locations (45% of total nest data), 207 sage-grouse early-brood locations (63% of total early-brood data), 93 sage-grouse late-brood locations (77% of total late-brood data), and 350 random locations (53% of total random data). Similar to the full analysis, avian predator variables did not covary with any other variable ($r^2 < 0.05$, VIF ≤ 2.3), indicating no multicollinearity between avian predator variables and anthropogenic or landscape feature variables. The subset analysis illustrated that the pattern of habitat use by sage-grouse was nearly the same as that in our full analysis in relation to avian predator densities and sage-grouse response to landscape attributes (Tables 6 and 7). Unlike in the full dataset, late-brood sage-grouse did not select for $SAGEpro_{1.0}$ or $RIP_{1.0}$; even so, the coefficients had the same positive values as in the full analysis (Table 7).

DISCUSSION

Sage-grouse hens used both indirect and direct mechanisms of predator avoidance to select habitat, which may have partially lowered their exposure to predation and nest predation. We did not quantify the effects of olfactory (mammalian) predators on sage-grouse selection of habitat. However, sage-grouse have not been found to hide their nests from olfactory predators at a microhabitat scale (Conover et al. 2010). In general, sage-grouse were located in less risky habitat that was farther away from potential perches and had lower densities of small, medium, and large avian predators. This result is largely concordant with the finding of Dinkins et al. (2012), who included some of the same bird location data but did not include landscape attribute or anthropogenic feature variables. The pattern of lower avian predator densities at sage-grouse locations was consistent between our full analysis and our analysis of locations >3 km away from anthropogenic structures (Tables 3 and 4 compared with Tables 6 and 7), which provided additional evidence that sage-grouse used direct predator avoidance. We found that sage-grouse locations were best described with models that included multiple habitat variables and avian predator densities. This implies that information on avian predator

TABLE 6. Multinomial logistic regression models comparing landscape-attribute variables and then comparing the top model from the landscape covariate set with the avian predator model (small, medium, and large avian predator densities) among locations used by sage-grouse (nest: $n = 153$, early-brood: $n = 207$, and late-brood: $n = 93$ locations) and random locations ($n = 350$) at 12 sites in southern Wyoming, USA, 2008–2011. Sage-grouse and random locations were greater than 3 km from anthropogenic features. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight. See Table 1 for variable descriptions.

Model	K	ΔAIC_c	w_i	Deviance
Landscape covariate set				
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$ [a]	15	0.00	0.75	1930.96
$SAGEpro_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	2.78	0.19	1939.96
$SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$	12	5.29	0.05	1942.46
$SAGEpro_{1.0}$, $NDVI_{0.27}$	9	8.50	0.01	1951.84
$RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	26.35	0.00	1963.52
$RIP_{1.0}$, $NDVI_{0.27}$	9	34.32	0.00	1977.66
$TRI_{0.54}$, $NDVI_{0.27}$	9	40.04	0.00	1983.38
$SAGEpro_{1.0}$, $RIP_{1.0}$	9	40.40	0.00	1983.74
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$	12	44.26	0.00	1984.44
$NDVI_{0.27}$	6	48.83	0.00	1998.30
Avian and landscape comparison				
Avian, landscape [b]	24	0.00	1.00	1715.40
Avian	12	109.55	0.00	1850.08
Landscape	15	196.64	0.00	1930.96
Intercept only	3	291.92	0.00	2050.82

[a] $AIC_c = 1961.57$.
[b] $AIC_c = 1764.93$.

use of sagebrush habitat, even sagebrush habitat little influenced by anthropogenic structures, could improve understanding of how sage-grouse are distributed in sagebrush habitat.

Sage-grouse exhibit high individual (among seasons) and generational site fidelity (Fisher et al. 1993, Holloran and Anderson 2005, Thompson 2012), which likely limits their ability to move in response to changing distributions of avian predators. Site fidelity has been suggested to delay nonuse patterns of sage-grouse in response to developing oil and gas fields, with older birds displaying strong fidelity despite low productivity and yearling birds (first nesting season) avoiding new anthropogenic structures (Holloran et al. 2010, Naugle et al. 2011). Older sage-grouse hens with failed nests in a previous nesting season had lower nest site fidelity compared with hens with successful nests (i.e. eggs hatched), but the average distances between their sequential nests were 512 m and 283 m, respectively, hardly landscape-level movements (Holloran and Anderson 2005). Distances between sequential nests from our study also indicated lower nest-site fidelity for hens with previously failed nests compared with hens with successful nests, especially when stratified by sites with low vs. high raven density (average distance to previously failed nests: 0.66 km [0.26 km SE] and 1.16 km [0.20 km SE], respectively; average distance to previously hatched nests: 0.53 km [0.20 km SE] and 0.36 km [0.08 km SE], respectively; Dinkins 2013). The greatest average distance between subsequent nests was for birds with previously failed nests in areas with comparatively higher raven density. Yearling birds seem to adjust spatial location at relatively large spatial extents, whereas older birds changed spatial location at smaller scales.

Rather than indirect and direct predator avoidance explaining our results, sage-grouse habitat use patterns could also be explained by areas of relatively greater predation over time leading to low sage-grouse productivity (i.e. sage-grouse disappear from a localized area, resembling nonuse by sage-grouse). It is plausible that our random locations were areas with greater avian predator densities associated with historically lower productivity for sage-grouse. Temporal stability in location of nesting structures for avian predators in sagebrush habitat could generate areas with greater predation risk for sage-grouse. However, stability also correlates with relatively constant spatial habitat use by avian predators, which might allow

TABLE 7. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 6). This analysis compares either nest, early-brood, or late-brood locations used by sage-grouse at 12 sites in southern Wyoming, USA, 2008–2011, with random (reference category) locations. See Table 1 for variable descriptions.

	Nest vs. random			Early-brood vs. random			Late-brood vs. random		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−7.83 (1.25)	−10.60	−5.69*	−20.30 (2.30)	−24.83	−15.77*	−19.98 (2.46)	−24.82	−15.13*
Small avian predator	−0.09 (0.05)	−0.18	<0.00*	−0.43 (0.10)	−0.62	−0.23*	−0.45 (0.12)	−0.69	−0.21*
Medium avian predator	−0.06 (0.03)	−0.11	<0.00*	−0.30 (0.05)	−0.39	−0.21*	−0.29 (0.06)	−0.40	−0.18*
Large avian predator	−0.13 (0.07)	−0.26	0.01	−0.73 (0.20)	−1.13	−0.34*	−0.40 (0.14)	−0.69	−0.12*
$SAGEpro_{1.0}$	3.65 (0.80)	2.07	5.23*	2.22 (0.74)	0.76	3.68*	0.29 (0.91)	−1.50	2.07
$RIP_{1.0}$	−0.85 (0.42)	−1.67	−0.03*	−0.06 (0.38)	−0.81	0.68	0.59 (0.49)	−0.38	1.56
$TRI_{0.54}$	−0.03 (0.01)	−0.04	−0.01*	−0.02 (0.01)	−0.03	<0.00*	−0.03 (0.01)	−0.05	−0.01*
$NDVI_{0.27}$	6.53 (1.50)	3.57	9.50*	6.01 (1.52)	3.02	8.99*	12.94 (1.72)	9.56	16.32*

* Denotes a 95% confidence interval that does not include zero.

sage-grouse to directly avoid them. Even small distance adjustments in sequential nest locations have the potential to move a sage-grouse outside of a corvid's or a raptor's home range or use hotspots. Lower nest-site fidelity of sage-grouse illustrates the capacity of sage-grouse to at least partially adjust their use of habitat by moving away from threats after nest failure. Our results indicate that sage-grouse habitat use patterns were likely a remnant of multiple factors. Predator avoidance (indirect and direct mechanisms) and localized disappearance of sage-grouse were unlikely to be mutually exclusive processes shaping habitat use patterns of sage-grouse.

Avian predators including *Buteo* hawks (MacLaren et al. 1988, Schroeder et al. 1999, Schroeder and Baydack 2001), Golden Eagles (MacLaren et al. 1988, Danvir 2002), harriers (Schroeder et al. 1999, Thirgood et al. 2000, Fletcher et al. 2003), kestrels (Schroeder et al. 1999), magpies (Holloran and Anderson 2003, Vander Haegen et al. 2002), and ravens (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010) negatively affect nest success or potentially prey on sage-grouse adults and chicks. One of the responses of prey species to the presence of these predators is direct avoidance (Lima 1998, Evans 2004, Cresswell 2008, Dinkins et al. 2012). Similarly to the results of Dinkins et al. (2012), our analyses indicated that sage-grouse avoided avian predators during all reproductive stages—nesting, early brood, and late brood—but at different magnitudes. Our results also suggest that sage-grouse hens have the ability to distinguish among threats to their own survival, their nests, and their offspring.

Sage-grouse are a relatively long-lived bird (Connelly et al. 2011). Johnson and Braun (1999) and Taylor et al. (2012) found that adult survival was the most influential demographic parameter on sage-grouse population growth, followed by chick survival and then nest success. Golden Eagles have been identified as the primary predator of adult sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006). Sage-grouse hens avoided Golden Eagles (large avian predators) at greater magnitudes than smaller avian predators within each reproductive stage (i.e. more strongly negative parameter estimates for large avian predators than for small and medium avian predators when comparing sage-grouse locations to random locations; Table 4), suggesting that sage-grouse hens were predominantly concerned with their own survival. Our results also indicated that the magnitudes of avian predator avoidance for predators of all sizes were greater at early-brood and late-brood locations than at nest locations, suggesting that broods moved in a way that reduced predation risk to both adults and chicks.

In addition to direct avoidance of avian predators, sage-grouse selected habitat in response to landscape attributes and anthropogenic features. Direct and indirect avoidance of avian predators were not necessarily linked (correlated) from the perspective of a sage-grouse, because indirect cues (perches and areas with food subsidies for predators) were not correlated with the density of any avian predator species ($r^2 < 0.02$). Similarly to previous research, our analyses confirmed that sage-grouse select locations farther away from landscape attributes that could be used as perches or provide subsidized food resources for predators, including oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) at all reproductive stages, power lines at brood locations, and major roads (Holloran 2005, Aldridge and Boyce 2007) and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. Sage-grouse also chose flatter locations, similarly to findings by Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). A greater proportion of big sagebrush and higher NDVI values were positively associated with sage-grouse locations. Greater proportion of sagebrush habitat has been positively correlated with abundance of sagebrush-obligate and associated birds including Brewer's Sparrows, Green-tailed Towhees (*Pipilo chlorurus*), sage-grouse, Sagebrush Sparrows, and Sage Thrashers (*Oreoscoptes montanus*; Knick et al. 2005, Noson et al. 2006, Aldridge et al. 2011). Sage-grouse population growth and recruitment have also been associated with a greater NDVI (Blomberg et al. 2012); however, Guttery et al. (2013) did not find a connection between NDVI values and sage-grouse chick survival.

Habitat use involves tradeoffs among risks of weather exposure and predation and benefits of food acquisition (Verdolin 2006). Similarly to the findings of Dzialak et al. (2011), our results confirmed that sage-grouse have opposing associations with riparian habitat depending on reproductive stage. Sage-grouse were farther away from riparian habitat compared with random locations while nesting, but were closer to it compared with random locations during late brood rearing. Nesting may have occurred away from riparian areas because concealment cover and lower predator abundance was more important than food availability for nesting sage-grouse hens. However, chicks have increasing energetic needs as they grow, and sage-grouse hens typically move broods to riparian areas after early brood rearing (Crawford et al. 2004, Gregg and Crawford 2009). Sage-grouse hens also move broods to align with changes in food availability as the breeding season progresses. Riparian habitats provide forbs and invertebrates that meet the energetic demands of growing sage-grouse chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011), but riparian habitats have a higher risk of brood failure (Aldridge and Boyce 2007). Sage-grouse appear to minimize the negative effects of increased predation risk associated with riparian areas directly by avoiding avian predators and indirectly by

avoiding riparian habitat during relatively more vulnerable reproductive stages (nest and early brood). Sage-grouse early-brood and late-brood locations were closer to rural houses than random and nest locations, which may be explained by the distribution of rural houses in more productive sagebrush habitat. This is speculative and deserves more research. If rural houses are in better habitat for brood foraging, sage-grouse movements to these areas may show similar patterns as movements to riparian habitat.

A prey species' ability to predict and avoid risky habitat increases survival and reproductive success, but the ability to directly avoid predators is more beneficial than avoiding indirect cues of predation risk (Thomson et al. 2006). Both mechanisms presumably achieve reduced predation rates; however, there may be other population-limiting effects as a result of indirect and direct predator avoidance, such as reduced foraging ability of prey species in areas of lower habitat quality (Lima 1998, Evans 2004, Cresswell 2008). High densities of avian predators and close proximity to landscape attributes and anthropogenic features—specifically riparian habitat, rugged topography, oil and gas infrastructure, power lines, and major roads—are likely to result in reduced adult survival and higher predation of sage-grouse eggs and chicks. Sage-grouse use of habitat was negatively associated with avian predator densities, with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. Increased avian predator abundance may induce changes in sage-grouse behavior associated with habitat usage. Thus, human manipulation of habitat that promotes increased densities of avian predators may limit sage-grouse populations, because even habitat that has high-quality cover and forage may become functionally unavailable to sage-grouse as avian predator densities increase.

ACKNOWLEDGMENTS

Research funding was provided by the Anadarko Petroleum Corporation, Jack H. Berryman Institute, Lincoln County Predator Management Board, Predatory Animal District of Sweetwater County, School of Energy Resources at the University of Wyoming, South Central and Southwest Wyoming Sage-grouse Local Working Groups, Utah Agricultural Experiment Station (Utah State University, publication number 8718), Uinta County Predator Management Board, Wyoming Animal Damage Management Board, and Wyoming Game and Fish Department. We greatly appreciate the logistical support provided by N. Tratnik, T. Christiansen, M. Zornes, N. Hymas, T. Clayson, M. Holloran, D. Oles, L. Oles, F. Blomquist, C. Morton, L. McCarthy, C. Powell, R. Etzelmiller, M. Murry, and many others. We thank our many field technicians, who are too numerous to name. We would also like to give a special thanks to the cooperation of the many landowners throughout southwestern and south-central Wyoming for allowing access to private lands.

LITERATURE CITED

Agresti, A. (2007). An Introduction to Categorical Data Analysis, second edition. John Wiley and Sons, Hoboken, NY, USA.

Aldridge, C. L. (2005). Identifying habitats for persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) in Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton, Canada.

Aldridge, C. L., and M. S. Boyce (2007). Linking occurrence and fitness to persistence: Habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

Aldridge, C. L., S. E. Hanser, S. E. Nielsen, M. Leu, B. S. Cade, D. J. Saher, and S. T. Knick (2011). Detectability adjusted count models of songbird abundance. In Sagebrush Ecosystem Conservation and Management: Ecoregional Assessment Tools and Models for the Wyoming Basins (S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge, Editors), Allen Press, Lawrence, KS, USA, pp. 141–220.

Anderson, D. R. (2008). Model Based Inference in the Life Sciences: A Primer on Evidence. Springer, New York.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bañuelos, M., M. Quevedo, and J. Obeso (2008). Habitat partitioning in endangered Cantabrian Capercaillie *Tetrao urogallus cantabricus*. Journal of Ornithology 149:245–252.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne (2012). Characteristics of climate and landscape disturbance influence the dynamics of Greater Sage-Grouse populations. Ecosphere 3:art55. http://dx.doi.org/10.1890/ES11-00304.1

Boarman, W. I. (1993). When a native predator becomes a pest: A case study. In Conservation and Resource Management (S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz, Editors), Pennsylvania Academy of Science, Easton, PA, USA, pp. 191–206.

Boarman, W. I., and B. Heinrich (1999). Common Raven (*Corvus corax*). In The Birds of North America 476 (F. B. Gill and A. Poole, Editors), Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington DC, USA.

Boarman, W. I., R. J. Camp, M. Hagan, and W. Deal (1995). Raven abundance at anthropogenic resources in the western Mojave Desert, California. Report to Edwards Air Force Base, California. National Biological Service, Riverside, CA, USA.

Bradley, L. C., and D. B. Fagre (1988). Coyote and bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322–327.

Braun, C. E. (1998). Sage grouse declines in western North America: What are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas (2001). Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, New York.

Bui, T. D., J. M. Marzluff, and B. Bedrosian (2010). Common Raven activity in relation to land use in western Wyoming:

Implications for Greater Sage-Grouse reproductive success. The Condor 112:65–78.
Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, second edition. Springer-Verlag, New York.
Carpenter, J., C. L. Aldridge, and M. S. Boyce (2010). Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.
Chalfoun, A. D., and T. E. Martin (2009). Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78: 497–503.
Coates, P. S., and D. J. Delehanty (2010). Nest predation of Greater Sage-Grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.
Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty (2014). Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: Implications for transmission line development. The Condor: Ornithological Applications 116. In press.
Connelly, J. W., C. A. Hagen, and M. A. Schroeder (2011). Characteristics and dynamics of Greater Sage-Grouse populations. Studies in Avian Biology 38:53–67.
Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver (2004). Conservation Assessment of Greater Sage-Grouse and Sagebrush Habitats. Unpublished Report, Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.
Conover, M. R., J. S. Borgo, R. E. Dritz, J. B. Dinkins, and D. K. Dahlgren (2010). Greater Sage-Grouse select nest sites to avoid visual but not olfactory predators. The Condor 112: 331–336.
Crawford, J. A., R. A. Olson, N. E. West, J. C Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd (2004). Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2–19.
Cresswell, W. (2008). Non-lethal effects of predation in birds. Ibis 150:3–17.
Danvir, R. E. (2002). Sage Grouse Ecology and Management in Northern Utah Sagebrush-Steppe. Deseret Land and Livestock Wildlife Research Report, Deseret Land and Livestock Ranch and the Utah Foundation for Quality Resource Management, Woodruff, UT, USA.
DeLong, J. P. (2004). Effects of Management Practices on Grassland Birds: Golden Eagle. Northern Prairie Wildlife Research Center, Jamestown, ND, USA.
Dinkins, J. D. (2013). Common Raven density and Greater Sage-Grouse nesting success in southern Wyoming: Potential conservation and management implications. Ph.D. dissertation, Utah State University, Logan, UT, USA.
Dinkins, J. D., M. R. Conover, C. P. Kirol, and J. L. Beck (2012). Greater Sage-Grouse (*Centrocercus urophasianus*) select nest-sites and brood-sites away from avian predators. The Auk 129:600–610.
Doherty, K. E. (2008). Sage-grouse and energy development: Integrating science with conservation planning to reduce impacts. Ph.D. dissertation, University of Montana, Missoula, MT, USA.
Doherty, K. E., D. E. Naugle, and B. L. Walker (2010). Greater Sage-Grouse nesting habitat: The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.
Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing (2011). Identifying and prioritizing Greater Sage-Grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273. doi:10.1371/journal.pone.0026273
Evans, K. L. (2004). The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.
Fedy, B., and K. Martin (2011). The influence of fine-scale habitat features on regional variation in population performance of alpine White-tailed Ptarmigan. The Condor 113:306–315.
Fisher, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly (1993). Nesting-area fidelity of Sage Grouse in southeastern Idaho. The Condor 95:1038–1041.
Fletcher, Q. E., C. W. Dockrill, D. J. Saher, and C. L. Aldridge (2003). Northern Harrier (*Circus cyaneaus*) attacks on Greater Sage-Grouse (*Centrocercus urophasianus*) in southern Alberta. Canadian Field-Naturalist 117:479–480.
Frey, S. N., and M. R. Conover (2006). Habitat use by meso-predators in a corridor environment. Journal of Wildlife Management 70:1111–1118.
Ghalambor, C. K., and T. E. Martin (2000). Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60: 263–267.
Giesen, K. M., T. J. Schoenberg, and C. E. Braun (1982). Methods for trapping Sage Grouse in Colorado. Wildlife Society Bulletin 10:224–231.
Gilbert, M. M., and A. D. Chalfoun (2011). Energy development affects populations of sagebrush songbirds in Wyoming. Journal of Wildlife Management 75:816–824.
Gregg, M. A., and J. A. Crawford (2009). Survival of Greater Sage-Grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.
Guttery, M. R., D. K. Dahlgren, T. A. Messmer, J. W. Connelly, K. P. Reese, P. A. Terletzky, N. Burkepile, and D. N. Koons (2013). Effects of landscape-scale environmental variation on Greater Sage-Grouse chick survival. PLOS One 8:e65582. doi:10.1371/journal.pone.0065582
Hanser, S. E., C. L. Aldridge, M. Leu, M. M. Rowland, S. E. Nielsen, and S. T. Knick (2011). Greater Sage-Grouse: General use and roost site occurrence with pellet counts as a measure of relative abundance. In Sagebrush Ecosystem Conservation and Management: Ecoregional Assessment Tools and Models for the Wyoming Basins (S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge, Editors), Allen Press, Lawrence, KS, USA, pp. 112–140.
Holloran, M. J. (2005). Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Ph.D. dissertation, University of Wyoming, Laramie, WY, USA.
Holloran, M. J., and S. H. Anderson (2003). Direct identification of northern sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.
Holloran, M. J., and S. H. Anderson (2005). Spatial distribution of Greater Sage-Grouse nests in relatively contiguous sagebrush habitats. The Condor 107:742–752.
Holloran, M. J., R. C. Kaiser, and W. A. Hubert (2010). Yearling Greater Sage-Grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Howe, K. B., P. S. Coates, and D. J. Delehanty (2014). Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem. The Condor: Ornithological Applications 116:35–49.

Johnson, K. H., and C. E. Braun (1999). Viability and conservation of an exploited sage-grouse population. Conservation Biology 13:77–84.

Kirol, C. P. (2012). Quantifying habitat importance for Greater Sage-Grouse (*Centrocercus urophasianus*) population persistence in an energy development landscape. M.S. thesis, University of Wyoming, Laramie, WY, USA.

Knick, S. T., A. L. Holmes, and A. F. Miller (2005). The role of fire in structuring sagebrush habitats and bird communities. Studies in Avian Biology 30:1–13.

Lammers, W. M., and M. W. Collopy (2007). Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. BioScience 48:25–34.

MacLaren, P. A., S. H. Anderson, and D. E. Runde (1988). Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

Manzer, D. L., and S. J. Hannon (2005). Relating grouse nest success and corvid density to habitat: A multi-scale approach. Journal of Wildlife Management 69:110–123.

Martin, T. E., and J. V. Briskie (2009). Predation on dependent offspring: A review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Annals of the New York Academy of Sciences 1168:201–217.

Mazerolle, M. J. (2012). Package 'AICcmodavg', version 1.25. R Foundation for Statistical Computing, Vienna. www.R-project.org

McCracken, M. L., B. F. J. Manly, and M. Vander Heyden (1998). The use of discrete-choice models for evaluating resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:268–279.

McDonald, T. L., B. F. J. Manly, R. M. Nielson, and L. V. Diller (2006). Discrete-choice modeling in wildlife studies exemplified by Northern Spotted Owl nighttime habitat selection. Journal of Wildlife Management 70:375–383.

Mezquida, E. T., S. J. Slater, and C. W. Benkman (2006). Sage-grouse and indirect interactions: Potential implication of coyote control on sage-grouse populations. The Condor 108: 747–759.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland (2011). Energy development and Greater Sage-Grouse. Studies in Avian Biology 38:489–503.

Noson, A. C., R. A. Schmitz, and R. F. Miller (2006). Influence of fire and juniper encroachment on birds in high elevation sagebrush steppe. Western North American Naturalist 66: 343–353.

Prather, P. R., and T. A. Messmer (2010). Raptor and corvid response to power distribution line perch deterrents in Utah. Journal of Wildlife Management 74:796–800.

Ralph, C. J., S. Droege, and J. R. Sauer (1995). Managing and Monitoring Birds using Point Counts: Standards and Applications. USDA Forest Service General Technical Report PSW-GTR-149.

R Development Core Team (2012). R: A Language and Environment for Statistical Computing, version 2.14.2. R Foundation for Statistical Computing, Vienna. www.R-project.org

Riley, S. J., S. D. DeGloria, and R. Elliot (1999). A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:1–4.

Schroeder, M. A., and R. K. Baydack (2001). Predation and the management of prairie grouse. Wildlife Society Bulletin 29: 24–32.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, et al. (2004). Distribution of sage grouse in North America. The Condor 106:363–376.

Schroeder, M. A., J. R. Young, and C. E. Braun (1999). Sage Grouse (*Centrocercus urophasianus*). In The Birds of North America 425 (F. B. Gill and A. Poole, Editors), Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington DC, USA.

Slater, S. J., and J. P. Smith (2010). Effectiveness of raptor perch deterrents on an electrical transmission line in southwestern Wyoming. Journal of Wildlife Management 74:1080–1088.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills (2012). Managing multiple vital rates to maximize Greater Sage-Grouse population growth. Journal of Wildlife Management 76:336–347.

Thirgood, S. J., S. M. Redpath, P. Rothery, and N. J. Aebischer (2000). Raptor predation and population limitation in Red Grouse. Journal of Animal Ecology 69:504–516.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, R. A. Marques, and K. P. Burnham (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson, T. R. (2012). Dispersal ecology of Greater Sage-Grouse in northwestern Colorado: Evidence from demographic and genetic methods. Ph.D. dissertation, University of Idaho, Moscow, ID, USA.

Thomson, R. L., J. T. Forsman, F. Sardà-Palomera, and M. Mönkkönen (2006). Fear factor: Prey habitat selection and its consequences in a predation risk landscape. Ecography 29: 507–514.

U.S. Department of Agriculture (2010). 2009 NAIP Survey: Summary Report. Farm Service Agency, Aerial Photography Field Office, Salt Lake City, UT, USA.

Vander Haegen, W. M., M. A. Schroeder, and R. M. DeGraaf (2002). Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. The Condor 104:496–506.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer (1992). An improved spotlighting technique for capturing Sage Grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L., D. E. Naugle, and K. E. Doherty (2007). Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Great Basin Naturalist

Volume 54 | Number 2 Article 10

4-29-1994

Brood habitat use by Sage Grouse in Oregon

Martin S. Drut
Oregon State University, Corvallis, Oregon

John A. Crawford
Oregon State University Corvallis, Oregon

Michael A. Gregg
Oregon State University, Corvallis, Oregon

Follow this and additional works at: https://scholarsarchive.byu.edu/gbn

Recommended Citation

Drut, Martin S.; Crawford, John A.; and Gregg, Michael A. (1994) "Brood habitat use by Sage Grouse in Oregon," *Great Basin Naturalist*: Vol. 54 : No. 2 , Article 10.
Available at: https://scholarsarchive.byu.edu/gbn/vol54/iss2/10

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Great Basin Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

Great Basin Naturalist 54(2), ©1994, pp. 170–176

BROOD HABITAT USE BY SAGE GROUSE IN OREGON

Martin S. Drut[1], John A. Crawford[1], and
Michael A. Gregg[1]

ABSTRACT.—Habitat use by Sage Grouse (*Centrocercus urophasianus*) hens with broods was examined at Jackass Creek and Hart Mountain, Oregon, from 1989 through 1991. Sage Grouse hens initially selected low sagebrush (*Artemisia* spp.) cover types during early brood-rearing, big sagebrush cover types later in the brood-rearing period, and ultimately concentrated use in and near lakebeds and meadows. Areas used by Sage Grouse broods typically had greater forb frequency than did random sites. Hens at Jackass Creek selected sites with forb cover similar to that generally available to broods at Hart Mountain, but home ranges were larger at Jackass Creek because of lower availability of suitable brood-rearing habitat. Differences in habitat use by broods on the two areas were reflected in dietary differences; at Hart Mountain, chicks primarily ate forbs and insects, whereas at Jackass Creek most of the diet was sagebrush. Larger home ranges, differences in diets, and differences in availability of forb-rich habitats possibly were related to differences in abundance and productivity between areas.

Key words: broods, Centrocercus urophasianus, *habitat, Oregon, Sage Grouse.*

Habitat factors, including resource availability, may limit Sage Grouse (*Centrocercus urophasianus*) populations through reduced recruitment of young (Klebenow 1969, Blake 1970, Wallestad 1975, Autenrieth 1981). Stand structure and food availability are characteristics most frequently associated with habitat selection by hens with broods (Klebenow 1969, Peterson 1970, Wallestad 1971, Autenrieth 1981). Dunn and Braun (1986) found that vegetative cover and extent of habitat interspersion are the most important factors influencing summer habitat use by Sage Grouse. Forbs and insects typically constitute the primary food of chicks (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994), and forb cover is often greater at sites used by broods than at random locations (Klebenow 1969, Autenrieth 1981, Dunn and Braun 1986). Shrubs, particularly sagebrush (*Artemisia* spp.), provide escape and thermal cover (Klebenow and Gray 1968) but are not a primary component of chick diets except where forbs and insects are limited in availability (Drut et al. 1994). Peterson (1970) noted decreased use of sagebrush/grassland cover types as broods mature and ascribed these changes to differential availability of succulent forbs. Martin (1970) observed that broods typically use big sagebrush (*A. tridentata*) stands during early brood-rearing and that broods <6 weeks old use areas with lower densities of sagebrush than do older broods.

Despite numerous studies of Sage Grouse summer habitat use, knowledge of habitat use and selection by Sage Grouse hens with broods is incomplete because of small sample sizes, lack of information about use and availability of cover types and habitat components within cover types used by hens with broods, failure to distinguish habitat use by hens with broods from other adults, or no provision of information regarding population status and habitat use. Information that relates population status and habitat use is critical for Oregon because the western subspecies (*C. u. phaios*), which inhabits most of the Sage Grouse range in the state, was listed as a candidate for threatened and endangered status by the Department of Interior in 1985. This listing resulted from declines in abundance caused by depressed productivity (Crawford and Lutz 1985). The objective of the study was to determine use of cover types and habitat components by Sage Grouse hens with broods during two brood-rearing periods on two study areas with different Sage Grouse population characteristics in southeastern Oregon.

[1]Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331-3803.

STUDY AREAS

The study was conducted at Jackass Creek, administered by the Bureau of Land Management, and Hart Mountain National Antelope Refuge, administered by the U.S. Fish and Wildlife Service. Estimates of Sage Grouse abundance since 1980 indicated approximately 2.5 birds/km^2 and 1.5 birds/km^2 at Hart Mountain and Jackass Creek, respectively (J. Lemos, Oregon Department of Fish and Wildlife, unpublished data; W. H. Pyle, U.S. Fish and Wildlife Service, unpublished data). Summer productivity counts from 1985 through 1992, the only period for which comparable data were available, averaged 1.6 and 0.9 chicks/hen ($p < .05$) at Hart Mountain and Jackass Creek, respectively.

The Jackass Creek study area, approximately 70 km southwest of Burns, Harney County, Oregon, comprises nearly 39,000 ha. Prominent shrubs are low sagebrush (*A. arbuscula*) and big sagebrush (*A. tridentata*). Western junipers (*Juniperus occidentalis*) are present on the eastern portion of the study area. Common annual and perennial forbs include mountain dandelion (*Agoseris* spp.), hawksbeard (*Crepis* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Grasses are principally bluegrass (*Poa* spp.) and fescue (*Festuca* spp.). Annual temperature averages 10°C, and mean precipitation is 25 cm.

The Hart Mountain National Antelope Refuge study area is 100 km southwest of Jackass Creek in Lake County, Oregon, and is 89,000 ha in size. Dominant cover consists of low sagebrush, big sagebrush, and antelope bitterbrush (*Purshia tridentata*). Areas >2000 m in elevation contain curl-leaf mountain-mahogany (*Cercocarpus ledifolius*) and trembling aspen (*Populus tremuloides*). Forb and grass composition is similar to Jackass Creek. At refuge headquarters (elevation 1700 m) annual temperature averages 6°C, and mean precipitation is 29 cm. Plant nomenclature follows Hitchcock and Cronquist (1987).

METHODS

Sage Grouse hens were radio-marked in 1989–91 (Gregg et al. 1994). At the conclusion of each field season, marked hens were recaptured, radio transmitters were removed, and a sample of previously unmarked hens was equipped with radios to maintain independence of samples among years. Radios were attached with herculite ponchos (Amstrup 1980), and all hens were fitted with numbered leg bands. Locations of radio-marked hens were obtained with portable receivers and two-element, hand-held antennae.

Cover types and habitat components used for rearing broods were identified from locations of radio-marked hens with broods. Radio-marked hens with broods were located four times weekly to identify cover types used. Monitoring of broods continued until a hen lost her brood or brood integrity disintegrated (approximately 1 August each year).

We classified cover at brood sites into one of seven cover types: big sagebrush, low sagebrush, mixed sagebrush, lakebed/meadow, mountain shrub, grassland, and juniper/aspen. Cover type descriptions were based on Soil Conservation Service information (J. Kinzel, U.S. Department of Agriculture, Soil Conservation Service, unpublished data) and previous descriptions at Jackass Creek (Trainer et al. 1983, Gregg 1992).

Study area boundaries, based on locations of radio-marked hens with broods, were determined each year with the minimum convex polygon method (Mohr 1947, Odum and Kuenzler 1955). Proportions of cover types within the area used for rearing broods were determined with a dot grid system (Avery 1977).

Each brood location was marked and served as a site for habitat sampling, which was completed within 2 days after location of a brood. Percent cover of forbs, grasses, and shrubs and frequency of occurrence of ground-dwelling insects were measured at all brood locations. We established two 10-m perpendicular transects intersecting at each brood location. The position of the first transect was determined from a randomly selected compass bearing. The intercept distance (cm) of all species of shrubs along each transect was recorded to determine canopy cover (Canfield 1941). Heights of shrubs intercepted were measured from the ground to the top of the shrub canopy and placed into one of three classes: short (<40 cm), medium (40–80 cm), or tall (>80 cm). Canopy cover of shrubs was recorded separately for each height class. Percent cover of forbs was estimated from five uniformly spaced rectangular plots (20 × 50 cm) on each transect (Daubenmire 1959).

Sampling intensity was determined by constructing a species area curve with data collected from initial sampling (Pieper 1978:12). Occurrence of ground-dwelling arthropods was established from 12 pitfall traps (Morill 1975) arranged systematically along each 23-m transect, 36 at Hart Mountain and 28 at Jackass Creek, in cover types used by broods (see Drut et al. 1994). Arthropods were classified into Scarabeidae (June beetles), Tenebrionidae (darkling beetles), Formicidae (ants), and other.

Vegetative structure of habitats available to Sage Grouse broods was characterized at randomly selected locations within cover types on each study area during the brood-rearing period. Sampling of random locations, which was concurrent with measurements taken at sites used by broods, was conducted during May and June of each year. Number of random locations sampled in each cover type was based on canopy cover of sagebrush, which represented the least variable habitat component, and was determined with the "n-test" (Snedecor and Cochran 1980:210).

Home ranges for hens with broods were determined with the McPaal home range program (Stuwe and Blohowiak 1983). Home ranges were compared for two brood-rearing periods (early: hatching to 6 weeks; and late: 7 to 12 weeks after hatching) within and between study areas with chi-square analysis (Snedecor and Cochran 1980:20). Six-week intervals were based on data from Martin (1970), which indicated hens with broods changed habitat use at this time, and from Peterson (1970), which revealed differences in foods consumed by juveniles beginning approximately 6 weeks after hatching.

Within study areas, cover types used by Sage Grouse for rearing broods were compared with availability of cover types. Between study areas, cover type availability and use were compared. We arranged data in contingency tables and analyzed them with chi-square analysis; cover types with <5 brood locations were combined and analyzed collectively. If differences were detected, confidence interval testing (Neu et al. 1974, Byers et al. 1984) was used to identify cover types used selectively. Use of cover types by hens with broods of different ages was compared with chi-square to assess possible changes in habitat use associated with age of broods. Cover types used for nesting by hens that successfully hatched clutches were compared with cover types used by hens with broods during the first 6 weeks after hatching.

Habitat components measured at brood sites were compared by chi-square analysis to random sites within the same cover types for each study area to identify which vegetative components were selected. Analysis of variance was used to test among cover types and between study areas for differences in availability (random locations) and use (brood locations) of vegetative cover (Snedecor and Cochran 1980:258). The least significant difference test was used to separate means (Snedecor and Cochran 1980:272). Results were considered significant at the 95% level.

RESULTS

Most broods (13) were produced in the big sagebrush cover type, but during early brood-rearing (hatching–6 weeks), hens with broods were most frequently found (54–67% of

TABLE 1. Use and availability of cover types in which Sage Grouse broods were produced and those used for early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	Jackass Creek					Hart Mountain				
	Used (% frequency)			Available (% of area)		Used (% frequency)			Available (% of area)	
Cover type	Hatched (N = 7)	Early (N = 7/84)[a]	Late (N = 3/40)[a]	Early	Late	Hatched (N = 11)	Early (N = 11/89)[a]	Late (N = 4/40)[a]	Early	Late
Big sagebrush	42	17	45	54	30	91	32	52	30	57
Low sagebrush	29	53	17	32	30	9	67	38	48	16
Mixed sagebrush	29	29	20	9	15	0	0	0	1	1
Lakebed/ meadow	0	0	15	3	23	0	0	8	3	5
Other	0	0	3	2	2	0	1	2	18	21

[a]Number of broods/number of locations.

observations) in low sagebrush cover (Table 1). Three cover types were used differentially during early brood-rearing: low sagebrush was used more ($p < .05$) than expected on both areas, mixed sagebrush was used in greater proportion ($p < .05$) than available at Jackass Creek, and big sagebrush was used to a lesser extent ($p < .05$) than available at Jackass Creek. None of the other cover types was used during the early brood-rearing period.

During late brood-rearing (7–12 weeks) habitat use shifted to predominantly big sagebrush (45–52% of observations). Use of low sagebrush declined on both areas (Table 1). Availability of low sagebrush within areas used by hens with broods declined from 48 to 16% at Hart Mountain as hens with broods moved away from low-sagebrush–dominated areas. Also, during late brood-rearing, use of lakebeds and meadows increased; these habitats received the greatest use after brood break-up in August.

Forb cover ranged from 10 to 14% at sites used by hens with broods during the early brood-rearing period (Table 2) and was greater ($p < .01$) at sites used by broods than at random locations at Jackass Creek. At Hart Mountain, forb cover was used in proportion to availability during early brood-rearing (Tables 2, 3). During late brood-rearing, forbs were used in greater ($p < .01$) proportion than available at Hart Mountain, where sites used by broods had 19–27% forb cover. No use pattern in relation to forb availability was evident at Jackass Creek during late brood-rearing. There were no differences in use and availability for any shrub cover category in low ($p > .50$), big ($p > .20$), or mixed ($p > .20$) sagebrush stands. Only in lakebed/meadow habitat at Jackass Creek during the late brood-rearing period were use and availability of shrub cover different ($p = .05$). In that instance, cover of short and medium shrubs was approximately twice as great at sites used by broods as at random locations (Tables 2, 3).

Hart Mountain had more forb cover ($p < .05$) and less tall shrub cover ($p < .05$) than Jackass Creek (Table 3). In addition, there was more ($p < .05$) short shrub cover available during the early brood-rearing period at Jackass Creek than at Hart Mountain. The greatest availability of forb cover on both areas was in lakebed/meadow habitat during late-brood-rearing (14 and 21% at Jackass Creek and Hart Mountain, respectively). Hart Mountain supported greater ($p < .01$) frequencies of ground-dwelling arthropods than did Jackass Creek, but no differences were found within study areas between time periods or cover types except at Jackass Creek, where mixed sagebrush had a greater ($p = .05$) frequency of invertebrates during the early period than did low sagebrush (Table 4).

At Hart Mountain, big sagebrush and lakebed/meadow habitats supported more ($p < .05$) forbs than did low sagebrush during late brood-rearing (Table 3). At Jackass Creek low and big sagebrush supported the same cover of forbs (6%) during late brood-rearing, but the lakebed/meadow habitat had greater ($p < .05$) forb cover (14%). There was more ($p < .05$) cover of medium and tall shrubs in big sagebrush stands compared with low sagebrush (Table 3).

Mean home range sizes at Hart Mountain, were 800 and 100 ha for the early and late periods, respectively, whereas at Jackass Creek mean home ranges were 2100 and 5100 ha, respectively. Home range size was smaller ($p = .02$) in the late period than the early period at Hart Mountain, whereas home range size increased ($p < .01$) during the late period at Jackass Creek. Home range size was smaller ($p < .01$) at Hart Mountain than at Jackass Creek during both periods.

DISCUSSION

Sage Grouse hens with broods displayed similar use of cover types on the two study areas. The change in cover-type use of successfully nesting hens from big sagebrush to low sagebrush during the first 6 weeks after hatching was unique to this study. Perhaps availability of foods partially accounted for this change in use of cover types. Klebenow (1969), Peterson (1970), Wallestad (1971), Autenrieth (1981), and Dunn and Braun (1986) reported relationships between habitat use by broods and food availability. Return to use of big sagebrush during weeks 7–12 after hatching was similar to findings elsewhere. Canopy cover and shrub height at brood sites in Montana changed from 6% and a range of 15–30 cm, respectively, in June to 12% and 30–45 cm in August (Peterson 1970). Pyrah (1971) and Wallestad (1971) noted sagebrush height was greater in cover types used by broods during

TABLE 2. Vegetative characteristics of sites within cover types used by Sage Grouse hens with broods during early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	% cover (SD)											
	Low sagebrush				Big sagebrush				Mixed sagebrush		Lakebed/meadow	
	Jackass Creek		Hart Mountain		Jackass Creek		Hart Mountain		Jackass Creek		Jackass Creek	Hart Mountain
Vegetative class	Early (N = 44)	Late (N = 7)	Early (N = 60)	Late (N = 15)	Early (N = 16)	Late (N = 18)	Early (N = 27)	Late (N = 21)	Early (N = 23)	Late (N = 7)	Late (N = 6)	Late (N = 3)
Forb	14 (5)	3 (1)	11 (3)	19 (5)	10 (4)	9 (3)	14 (5)	19 (4)	14 (4)	12 (4)	2 (3)	27 (9)
Grass	8 (4)	3 (1)	14 (5)	17 (6)	10 (4)	11 (8)	15 (7)	16 (8)	9 (6)	9 (5)	6 (4)	1 (1)
Shrub												
Short (<40 cm)	25 (7)	36 (9)	22 (8)	19 (9)	5 (3)	5 (3)	18 (9)	17 (9)	21 (8)	13 (8)	23 (13)	0
Medium (40–80 cm)	1 (1)	0	0	0	15 (7)	14 (7)	9 (10)	14 (17)	6 (6)	12 (7)	20 (13)	0
Tall (>80 cm)	0	0	0	0	2 (4)	4 (5)	0	0	1 (1)	4 (11)	0	0

TABLE 3. Vegetative characteristics of available cover in habitats used by Sage Grouse during early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91

	% cover (SD)											
	Low sagebrush				Big sagebrush				Mixed sagebrush		Lakebed/meadow	
	Jackass Creek		Hart Mountain		Jackass Creek		Hart Mountain		Jackass Creek		Jackass Creek	Hart Mountain
Vegetative class	Early (N = 74)	Late (N = 50)	Early (N = 80)	Late (N = 56)	Early (N = 51)	Late (N = 20)	Early (N = 72)	Late (N = 30)	Early (N = 51)	Late (N = 30)	Late (N = 25)	Late (N = 20)
Forb	9 (5)	6 (2)	10 (4)	8 (3)	9 (6)	6 (2)	13 (6)	14 (5)	6 (4)	3 (2)	14 (14)	21 (17)
Grass	6 (3)	6 (3)	11 (6)	12 (7)	10 (6)	8 (3)	12 (6)	13 (7)	7 (5)	6 (4)	4 (5)	1 (1)
Shrub												
Short (<40 cm)	24 (8)	28 (10)	18 (8)	21 (9)	5 (4)	8 (6)	17 (11)	17 (9)	8 (10)	21 (8)	11 (10)	0
Medium (40–80 cm)	1 (1)	0	0	0	12 (6)	13 (7)	17 (12)	16 (11)	5 (5)	9 (6)	10 (10)	0
Tall (>80 cm)	0	0	0	0	5 (6)	9 (10)	1 (2)	1 (4)	3 (7)	2 (3)	0	0

TABLE 4. Frequencies of occurrence (%) of major insect groups available during early (hatching–6 weeks) and late (7–12 weeks) Sage Grouse brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	Low sagebrush				Big sagebrush			Mixed sagebrush	
	Jackass Creek		Hart Mountain		Jackass Creek	Hart Mountain		Jackass Creek	
Family	Early (N = 102)	Late (N = 84)	Early (N = 120)	Late (N = 36)	Early (N=12)	Early (N = 60)	Late (N = 36)	Early (N = 60)	Late (N = 60)
Scarabeidae	1	0	10	14	0	4	9	0	0
Tenebrionidae	11	8	17	14	28	16	27	15	12
Formicidae	42	47	68	62	42	81	76	61	41
Other	49	38	70	74	37	97	96	52	51

late summer; sagebrush canopy cover used by hens with broods changed from 14% in June to 21% in September (Pyrah 1971).

Cover types used by hens with broods typically had greater availability of forbs during periods of high use, but differences in availability between areas influenced use of cover types, movements, and diets. Hens at Jackass Creek selectively used sites with forb cover greater than typically found there and similar to that generally available to broods at Hart Mountain. This amount of forb cover (12–14%) may represent the minimum needed for brood habitat in Oregon. The lack of a relationship between brood use and forb availability during the late brood-rearing period at Jackass Creek likely was related to the dietary shift by chicks to sagebrush during this time (Drut et al. 1994).

Home ranges of hens with broods were larger at Jackass Creek than at Hart Mountain and increased over time. May and Poley (1969) observed no movements from meadows until fall in Colorado, and in Montana brood home ranges decreased from 85 ha in June to 51 ha in August (Wallestad 1971). The large home ranges at Jackass Creek reflected differences in forb availability and chick diets between areas (Drut et al. 1994). Chicks consumed primarily forbs and insects at Hart Mountain but ate mostly sagebrush at Jackass Creek (Drut et al. 1994). Home ranges in Idaho were larger for hens with broods than for broodless hens (406 ha and 174 ha, respectively), which possibly was related to forb use (Connelly and Markham 1983). These authors also noted that Sage Grouse may occupy larger summer home ranges in wet years because of greater availability of forbs. Differences in availability of brood-rearing habitats, dietary intake of chicks, and home range sizes perhaps are related to differences in productivity and abundance of Sage Grouse at the two study areas.

ACKNOWLEDGMENTS

This project was supported by a research contract from the Bureau of Land Management and administered by the Oregon Department of Fish and Wildlife. We acknowledge the assistance of E. G. Campbell. J. W. Connelly, A. K. DeLong, W. D. Edge, and R. L. Jarvis reviewed the manuscript. This is publication 10269 of the Oregon Agricultural Experiment Station.

LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. Journal of Wildlife Management 44: 214–217.

AUTENRIETH, R. E. 1981. Sage Grouse management in Idaho. Idaho Department of Fish and Game. Wildlife Bulletin 9. 238 pp.

AVERY, T. E. 1977. Interpretation of aerial photographs. 3rd edition. Burgess Press, Minneapolis, Minnesota. 391 pp.

BLAKE, C. S. 1970. The response of Sage Grouse to precipitation trends and habitat quality in south central Idaho. Proceedings of the Western Association of the State Game and Fish Commissioners 50: 452–462.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48: 1050–1053.

CANFIELD, R. 1941. Application of the line interception method in sampling of range vegetation. Journal of Forestry 39: 386–394.

CONNELLY, J. W., AND O. D. MARKHAM. 1983. Movements and radionuclide concentrations of Sage Grouse in southeastern Idaho. Journal of Wildlife Management 47: 169–177.

CRAWFORD, J. A., AND R. S. LUTZ. 1985. Sage Grouse population trends in Oregon, 1941–1983. Murrelet 66: 69–74.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33: 224–227.

DRUT, M. S., W. H. PYLE, AND J. A. CRAWFORD. 1994. Diets and food selection of Sage Grouse chicks in Oregon. Journal of Range Management 47: 90–93.

DUNN, P. O., AND C. E. BRAUN. 1986. Summer habitat use by female and juvenile Sage Grouse. Journal of Wildlife Management 50: 228–235.

GREGG, M. A. 1992. Use and selection of nesting habitat by Sage Grouse in Oregon. Unpublished master's thesis, Oregon State University, Corvallis. 46 pp.

GREGG, M. A, J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. Journal of Wildlife Management 58: 162–166.

HITCHCOCK, C. L., AND A. CRONQUIST. 1987. Flora of the Pacific Northwest. 6th edition. University of Washington Press, Seattle. 730 pp.

KLEBENOW, D. A. 1969. Sage Grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33: 649–662.

KLEBENOW, D. A., AND D. M. GRAY. 1968. Food habits of juvenile Sage Grouse. Journal of Wildlife Management 12: 80–83.

MARTIN, N. S. 1970. Sagebrush control related to habitat and Sage Grouse occurrence. Journal of Wildlife Management 34: 313–320.

MAY, T. A., AND B. E. POLEY. 1969. Spring and summer movements of female Sage Grouse in North Park, Colorado. Proceedings of the Western States Sage Grouse Workshop 6: 173–179.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223–249.

MORILL, W. L. 1975. Plastic pitfall trap. Environmental Entomology 4: 596.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization data. Journal of Wildlife Management 38: 541–545.

ODUM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72: 128–137.

PETERSON, J. G. 1970. The food habits and summer distribution of juvenile Sage Grouse in central Montana. Journal of Wildlife Management 34: 147–155.

PIEPER, R. D. 1978. Measurement techniques for herbaceous and shrubby vegetation. New Mexico State University Press, Las Cruces. 148 pp.

PYRAH, D. B. 1971. Sage Grouse research in central Montana. Proceedings of the Western Association of the State Game and Fish Commissioners 51: 293–300.

SNEDECOR, G. W., AND R. G. COCHRAN. 1980. Statistical methods. 7th edition. Iowa State University Press, Ames. 507 pp.

STUWE, M., AND C. E. BLOHOWIAK. 1983. McPaal—micro-computer programs for the analysis of animal locations. Smithsonian Institution, Washington, D.C. 20 pp.

TRAINER, C. E., M. J. WILLIS, G. P. KEISTER, AND D. P. SHEEHY. 1983. Fawn mortality and habitat use among pronghorn during spring and summer in southeastern Oregon, 1981–82. Oregon Department of Fish and Wildlife, Wildlife Research Report 12. 117 pp.

WALLESTAD, R. O. 1971. Summer movement and habitat use by Sage Grouse broods in Montana. Journal of Wildlife Management 35: 129–136.

_____. 1975. Life history and habitat requirements of Sage Grouse in central Montana. Game Management Division, Montana Department of Fish and Game, Helena. 66 pp.

Received 2 September 1993
Accepted 4 January 1994

The Geological Society of America
Special Paper 562

GOLD OPEN ACCESS

Impacts of beaver dams on riverscape burn severity during megafires in the Rocky Mountain region, western United States

Emily Fairfax
Department of Geography, Environment, and Society, University of Minnesota Twin Cities, 267 S 19th Avenue, Minneapolis, Minnesota 55455, USA

Alexa Whipple
Methow Beaver Project, 50 Twisp River Road, Twisp, Washington 98856, USA

Joe M. Wheaton
Department of Watershed Sciences, Utah State University, 0160 Old Main Hill, Logan, Utah 84322-0160, USA

Brandon Osorio
Joe Miller
Keitreice Kirksey
Natalie Perez
Department of Environmental Science and Resource Management, California State University Channel Islands, 1 University Drive, Camarillo, California 93012, USA

Jordan T. Gilbert
Department of Watershed Sciences, Utah State University, 0160 Old Main Hill, Logan, Utah 84322-0160, USA

Chris E. Jordan
National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 2032 SE OSU Drive, Newport, Oregon 97365, USA

ABSTRACT

Megafires, defined as fires with burn areas greater than 100,000 acres (404.7 km^2), result partly from increasingly short wet seasons coupled with consistently hotter, drier summers, and partly from past forest management decisions. Historically rare, megafires have become increasingly common in recent years. In this study, we examined the impact of megafires on riverscapes with beaver dams to explore the resilience of these habitats. We investigated whether beaver-modified riverscapes are more resistant to the impacts of megafires than geomorphically similar riverscapes lacking beaver dams. Our analysis utilized remotely sensed and field-collected data from three Rocky Mountain region megafires that burned in 2020. Our results showed that riparian areas with beaver dams (1537 beaver dams, which occurred in 658 out of

Fairfax, E., Whipple, A., Wheaton, J.M., Osorio, B., Miller, J., Kirksey, K., Perez, N., Gilbert, J.T., and Jordan, C.E., 2024, Impacts of beaver dams on riverscape burn severity during megafires in the Rocky Mountain region, western United States, *in* Florsheim, J.L., O'Dowd, A.P., and Chin, A., eds., Biogeomorphic Responses to Wildfire in Fluvial Ecosystems: Geological Society of America Special Paper 562, p. 131–151, https://doi.org/10.1130/2024.2562(07). © 2024 The Authors. Gold Open Access: This chapter is published under the terms of the CC-BY-NC license and is available open access on www.gsapubs.org.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

13,933 valley bottom segments evaluated) had significantly reduced burn severity compared to riverscapes without beaver dams or to areas outside the river corridor. Additionally, when riverscapes were classified according to their modeled beaver dam capacities (a metric closely linked to riparian habitat quality), areas with beaver dams had consistently lower burn intensities than those without beaver dams, even within the same theoretical dam capacity class. Our results indicate that riverscapes with a high degree of manipulation by beavers have significant resistance to burning during megafires. This resistance may also provide valuable secondary benefits in postfire ecosystem health, water quality, and biodiversity.

1. INTRODUCTION

1.1. Impacts of Megafires on People and Ecosystems

This study defines megafires as fires with burn areas greater than 100,000 acres (404.7 km^2; Linley et al., 2022), consistent with the National Interagency Fire Center. These large and often highly destructive fires are partially the result of increasingly short wet seasons coupled with hotter, drier summers, year after year (Goss et al., 2020; Khorshidi et al., 2020; Swain, 2021; Syphard et al., 2007). Though megafires historically were rare, they have become increasingly common in recent years (Le Breton et al., 2022). These fires pose unique challenges: They have exceptionally fast rates of spread; they generate self-sustaining weather systems; and they can easily cause secondary ignitions in the surrounding landscape via ember spotting and lightning strikes from pyrocumulus clouds (Rodriguez et al., 2020; Stephens et al., 2014; Williams, 2013). These features culminate in an environment where the fire perimeter expands rapidly, posing significant risks to both humans and ecosystems (Williams, 2013).

Megafires are most common when two conditions are met: (1) There is severe fire weather (extreme heat, high winds, and convective instability; Prein et al., 2016), and (2) the landscape is predisposed toward intense and fast-spreading fires (Coen et al., 2018; Khorshidi et al., 2020; Stephens et al., 2014; Williams, 2013). Megafires have been linked to increasingly intense, long periods of severe fire weather fueled by climate change. At the same time, the role that forest management plays in making landscapes more or less susceptible to megafires remains understudied (Williams, 2013). Megafires are far less common than smaller wildfires, but they account for a disproportionately large amount of property damage, habitat destruction, fatalities, and fire-fighting costs (Jones et al., 2021; Williams, 2013). Land-management agencies have traditionally taken two approaches for addressing the rise of megafires: (1) aggressively increase the scale of fire-suppression efforts during the events, or (2) take preventative measures to reduce the likelihood that a megafire can form. Megafires often outpace containment efforts until large, naturally occurring fuel breaks or weather changes disrupt them. Scaling up the fire-fighting force alone has not been successful. The year 2020 was among the worst fire years on record in terms of property damage and lives lost, and most of those losses occurred in megafires (Goss et al., 2020; Higuera and Abatzoglou, 2021; Swain, 2021). Therefore, shifting a portion of fire-management focus to making landscapes less favorable for megafires seems to be a prudent course of action.

Although it takes only one day of severe fire weather to start a megafire, it can generate its own hot, dry, windy weather system once initiated. Megafires, therefore, can create a positive feedback cycle of self-intensifying fire expansion, posing a major challenge for containment (Rodriguez et al., 2020). Wind spreads the fire at fast rates and enables long-distance fire spotting (ignition) from wind-driven embers. The air around megafires is dried to critically low humidities, which in turn rapidly desiccates any available fuel that is not actively being irrigated. Dry fuels and high wind allow the fire to rapidly expand (Coen et al., 2018; Khorshidi et al., 2020; Williams, 2013). As it does, the air gets drier, and the winds get stronger, further accelerating the spread of the fire and promoting a positive feedback loop. According to Williams (2013), landscapes are particularly prone to severe burning due to megafires under one or more of the following conditions (adapted from Williams, 2013):

(1) Biomass and fuel accumulations dominate the landscapes;
(2) rivers are disconnected from their floodplains;
(3) woody debris and riparian vegetation are largely removed from floodplains;
(4) wetlands are drained;
(5) large, late successional stands are prioritized for recreation and aesthetics rather than fire prevention or resilience; and/or
(6) vegetation mosaics are diminished, becoming more continuous high-hazard landscapes.

To help reduce the risk of excessive burning due to megafires, recommended practices for land-management agencies aim to achieve the opposites of these conditions. A landscape resistant to megafires would then have the following characteristics:

(1) Fuel and biomass are regularly removed by natural processes (e.g., low-intensity managed or natural fires, herbivory, or mechanical methods such as thinning or back-burning/burnout to remove excess fuels in the face of wildfire);
(2) rivers are well connected to their floodplains;
(3) large wood is present across floodplain surfaces;

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

(4) wetlands are reestablished;
(5) strategic areas prioritize low-flammability new growth; and/or
(6) vegetation mosaics are restored, and patch size of individual land-cover types is reduced.

Conditions to reduce risk of megafire can all be met through the reestablishment of healthy biologic and fluvial-geomorphic processes in watersheds. This suite of processes is broadly needed on watershed scales across North America to address the last two centuries of human impacts (Wohl et al., 2021). Nature-based, and specifically natural process–based, restorations of watersheds, including the activities of beavers, are cost-effective, scalable, low-tech, durable methods to return the natural function and resilience to rivers, streams, riparian areas, wetlands, and groundwater systems at the landscape scale (Jordan and Fairfax, 2022; Skidmore and Wheaton, 2022; Wheaton et al., 2019; Wohl et al., 2015).

1.2. Riverscapes as Climate-Resilient Natural Infrastructure

Large rivers already are utilized as fire breaks in small- to medium-sized fires. Fire-management plans take advantage of the fact that water does not burn. Riverscapes include far more than just the river channel itself. They include the floodplains, the wetlands, the wet meadows, the side channels, the subsurface hyporheic zone, and the shallow groundwater systems historically created and maintained by widespread native beaver activity across most river valley bottoms. In a functioning riverscape, these elements increase wetted area and fire resistance and refugia. Beavers, and their innate ecosystem engineering behaviors, are uniquely capable of restoring and rewetting riverscapes even under highly modified and simplified modern stream and river conditions. Key characteristics of functional riverscapes include the capacity for adjustment; structural forcing gained from wood jams, dams, and living vegetation; and flow-energy dissipation (Castro and Thorne, 2019; Wheaton et al., 2019). Together, these elements form a dynamic fluvial biogeomorphic system of positive feedback cycles that builds complex, wet, climate-resilient riverscapes (Wohl, 2021a; Wohl et al., 2021). In general, the structural forcing elements are biologically based (living vegetation and dead vegetation both typically increase as a result of beaver activity) and thus represent a continual input of energy (the biological processes) to the fluvial-geomorphic processes, thereby tying the transport-deposition state of a riverscape to the balance of its physical and biological processes (Johnson et al., 2019; Phillips, 2009, 2016). Thus, the climate resilience of wetted functional riverscapes is dependent on natural process complexity.

When degraded, riverscapes simplify to stable, dry, disconnected systems typically dominated by incised, high-energy single-threaded channels (Cluer and Thorne, 2014). The balance of the fundamental physical and ecological processes commonly shifts to a stable but functionally impaired state, where the lack of structural forcing leads to decreased lateral and vertical channel adjustment. Restoration of the function and form of degraded and simplified riverscapes has presented a distinct challenge to traditional form-based restoration approaches driven by engineering design (Wohl et al., 2015). Process-based restoration is a conceptual framework arguing for the management of processes, not form, when engaging in stream habitat restoration planning (Thompson and Stull, 2002; Beechie et al., 2010).

Low-tech process-based restoration (LT-PBR) is founded on a suite of well-established restoration principles within the process-based restoration paradigm (Wheaton et al., 2019). This approach emphasizes promoting natural processes in rivers with simple structural additions built from natural materials, rather than designing and building the riverscapes ourselves with extensive engineering or heavy machinery (Ciotti et al., 2021). Forming a partnership with beavers, and relying largely on them to do the physical work to restore riverscapes, is an established LT-PBR strategy that minimizes human time and effort and maximizes the reliance on natural ecohydrologic and biogeomorphic processes (Brazier et al., 2021; Dittbrenner et al., 2018; Jordan and Fairfax, 2022; Law et al., 2017; Macfarlane et al., 2015; Pollock et al., 2014, 2015; Scamardo and Wohl, 2019).

Numerous resources already exist to provide guidance on how, where, and at what cost restoration efforts can utilize LT-PBR strategies on a case-by-case basis (Dittbrenner et al., 2018; Macfarlane et al., 2015; Wheaton et al., 2019; Norman et al., 2022). While historically, LT-PBR has been used to improve fish habitat and water quality, the potential for its direct use as a fire-mitigation strategy is theoretically sound but lacking in application. Such restoration may support the desired landscape conditions that contribute to reduced megafire risk and increased fire refugia area by increasing channel and floodplain complexity and altering streamflow. They may additionally be enhanced by combining these LT-PBR strategies with current typical fire risk-reduction activities, such as fuel thinning, burnouts, and grazing management coupled with fuel thinning for understory maintenance, as described in Table 1, to further reduce risk.

Changing or increasing the scope and scale of human-based fire management is a multidimensional process involving prioritization in policy, budgets, and personnel. By allowing beavers to engage in natural ecosystem engineering behaviors, the scope and scale of restoration and the resulting climate resilience can increase with less human intervention (Law et al., 2017).

1.3. Does Beaver Ecosystem Engineering Accelerate and Expand Riverscape Restoration and Resilience?

Beavers, a keystone species, engineer their environment through the construction of leaky dams, coppicing or pruning trees and shrubs, and digging travel canals (Brazier et al., 2021; Larsen et al., 2021; Naiman et al., 1988; Pollock et al., 1995). Although beavers do this work to ensure a safe, stable habitat for themselves, these activities have significant impacts on the geomorphology and ecohydrology of riverscapes. Dams slow water down, create ponds, and induce more regular overbank flooding, and they

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 1. COMPARISON OF STRATEGIES FOR INCREASING LANDSCAPE RESILIENCE TO FIRE THROUGH CURRENT TYPICAL FIRE MANAGEMENT, LOW-TECH PROCESS-BASED RESTORATION (LT-PBR), AND A COMBINATION OF PRACTICES

Desired landscape conditions	Current typical fire management techniques	LT-PBR of riverscapes	Current typical fire management techniques coupled with LT-PBR
Fuels and excess biomass are regularly removed from landscape. Debris is added to aquatic portions of watersheds.	Mechanical fuel thinning, prescribed burning for removing fuels, N/A for debris added to aquatic portions of watersheds.	Periodic flooding near in-stream structures mobilizes downed fuels and debris. Woody debris is added to river channels and floodplains to initiate natural, self-sustaining processes.	Mechanically thinned fuels are added to river channels as structures or building materials for beavers, forcing more complex pathways for conveyance of water and increasing inundated surface area while increasing the area from which the waterway can remove additional fuels and debris. Positive feedback cycle of riverscape restoration and fire resilience is established.
Wetlands are established. Low-flammability new growth is prioritized in strategic areas.	N/A for wetland establishment, prescribed or cultural burning for prioritizing new growth.	Beaver-based restoration creates and maintains wetlands throughout riverscapes. Can be accomplished with live beavers, beaver dam analogs, or a combination of the two. Beavers coppice or prune riparian trees regularly, which removes old growth vegetation, transports woody biomass into the rivers, and promotes the growth of younger, less flammable vegetation. Periodic flooding encourages new growth across the entire floodplain.	Riparian corridors rapidly regain the ability to withstand large-scale disturbances via LT-PBR. Prescribed burning can extend the buffer zone via strategic application near waterways and/or between patches of restored riverscape. Culminates in longer, wider, and more contiguous stretches of low-flammability, wet fuels.
Vegetation mosaics are established, increasing overall landscape disturbance resilience.	Prescribed or cultural burning with or without strategic reseeding.	Diverse habitats are naturally established and sustained within restored riverscapes.	Vegetation mosaics are broadly established and maintained both within riverscapes and surrounding landscapes.

contribute to groundwater recharge (Andersen and Shafroth, 2010; Feiner and Lowry, 2015; Lowry, 1993; Puttock et al., 2021; Westbrook et al., 2006). The canals help spread that water out throughout the floodplain, increasing the area influenced by beaver ecosystem engineering (Anderson et al., 2015; Hood and Larson, 2015; Bartelt, 2021). The combination of canal digging and dam building contributes to significantly more water storage both in the surface water system as well as subsurface in the nearby soils, even during dry periods. When beavers coppice trees and shrubs, they keep the ecosystem in a constant state of new growth and actively move large woody material from the broader adjacent landscape into the river and stream channels (Hyvönen and Nummi, 2008; Kirby et al., 2017; Rood and Mahoney, 1990). The presence of woody material in rivers—including beaver dams, lodges, and food caches—increases geomorphic and hydrologic complexity (Bashinskiy, 2020; Gurnell, 1998; MacCracken et al., 2005; Magilligan et al., 2008; Osei et al., 2015; Wohl, 2015; Wohl and Scott, 2016). This complexity accelerates process restoration and builds resilience to disturbances like flood, drought, and wildfire throughout a beaver's typical 1–2 km territory along a stream or river segment (Fairfax and Small, 2018; Fairfax and Whittle, 2020; Foster et al., 2020; Hillman, 1998; Hood and Bayley, 2008; Jordan and Fairfax, 2022; Puttock et al., 2021; Westbrook et al., 2006, 2020; Whipple, 2019).

Research shows the benefits and efficacy of beaver activity and beaver mimicry in the restoration of riverscapes. A factor that has not been explored is whether beaver-engineered climate resilience in riverscapes is maintained during the increasingly extreme wildfire behaviors that occur during megafires. Therefore, this study explored the extent to which beaver-modified areas are resistant to megafires. Additionally, we investigated whether this type of climate resilience is attributable to beaver activity or to a geomorphic setting that is itself conducive to beaver dam- and canal-building activity.

We hypothesized (H) that during megafires:

(H1) riverscapes have lower burn severity than the rest of the landscape,

(H2) beaver-dammed riverscapes have lower burn severity than riverscapes without beaver dams, and

(H3) riverscapes with a higher capacity for beaver dams have lower burn severity than those with a lower capacity for beaver dams, driving increased climate resilience during extreme disturbance events.

2. STUDY AREA

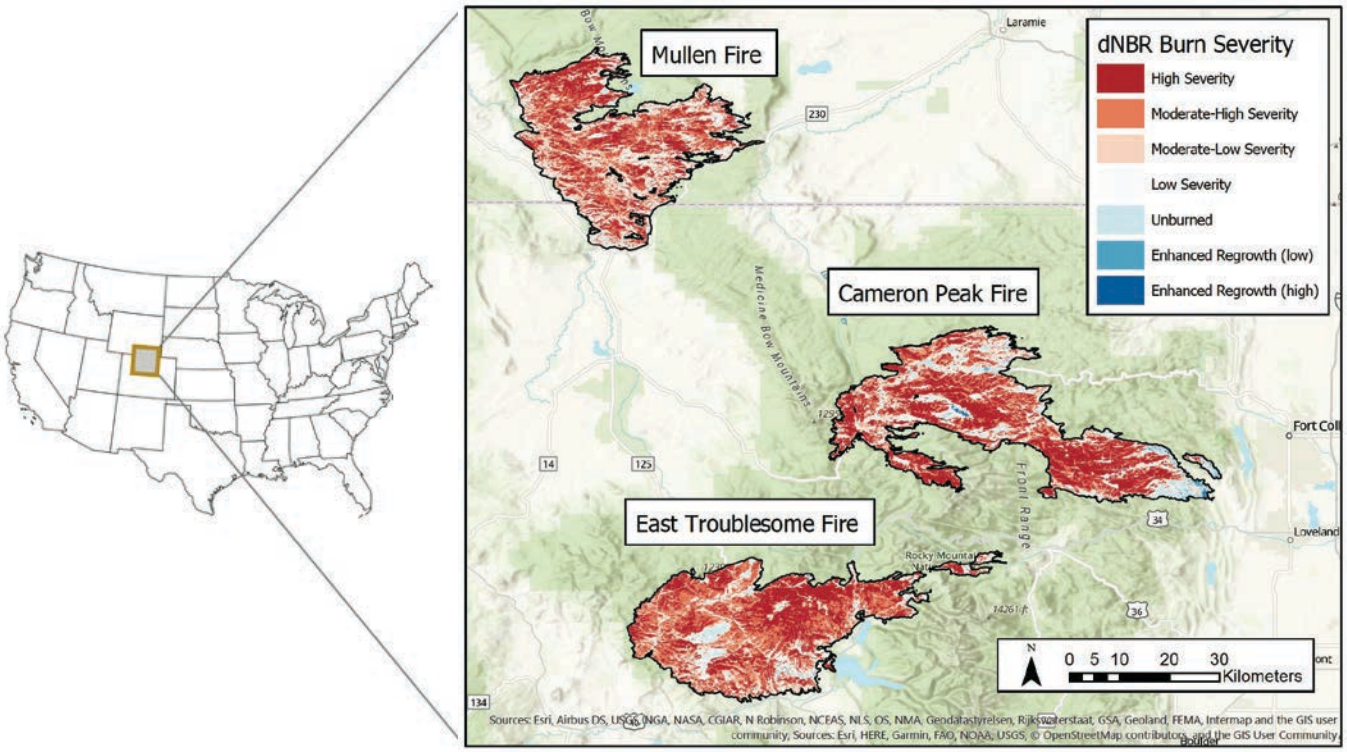
This study included three megafires that occurred in 2020 in the Rocky Mountain region, western United States: Cameron

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

Peak (Colorado), East Troublesome (Colorado), and Mullen (Wyoming) (Fig. 1). Fire perimeters were downloaded as shapefiles from the National Interagency Fire Center (NIFC, 2022). Table 2 reports detailed information about each fire, including the area within the burn perimeter, the states and counties affected, the burn dates, the standardized precipitation evapotranspiration index (SPEI) drought conditions leading up to the fires (Vicente-Serrano et al., 2010), the 2019 National Land Cover Database dominant land-cover type (NLCD 2019 *in* Dewitz and USGS, 2021), and the number of satellite-visible beaver dams within each fire perimeter. Wildfires can be large in area but not necessarily destructive or damaging to ecosystems. In the American West, many landscapes are dependent on fire and should be burning regularly (Agee, 1998; Bowman et al., 2011; Dwire and Kauffman, 2003; Skinner and Chang, 1996; Syphard et al., 2007). These three fire locations exemplify fire-adapted, semi-arid, montane to alpine mixed conifer forest that historically experienced high-frequency, low-severity fire regimes but have been subject to systematic fire suppression and inadequate forest management for the last century. All three megafires included in this study exhibited extreme fire behavior outside of the natural fire regime. Each had varying amounts of satellite-visible beaver activity within their perimeters. The Cameron Peak Fire had the least amount of beaver activity, and it tended to occur in isolated pockets along the river network. The East Troublesome Fire had more beaver activity, and it was more distributed throughout the river network. The Mullen Fire had the most beaver activity, and the majority of the river network was influenced by beaver ecosystem engineering.

3. METHODS

We applied three lines of evidence (described below) to test our three hypotheses on the wildfire resilience of riverscapes and beaver-modified riverscapes in the face of megafires in the Rocky Mountain region. First, we quantified burn severity using the remotely sensed differential normalized burn ratio (dNBR), and we qualitatively assessed burn severity with false-color imagery and field photographs. Next, we sampled data within and outside of the riverscapes. Finally, we further stratified the riverscape data by its extant beaver dam-building activity and theoretical beaver dam capacity provided by the Beaver Restoration Assessment Tool (BRAT; Macfarlane et al., 2015) model.



Cameron Peak Fire: 40.641731 °N, 105.674679 °W
East Troublesome Fire: 40.228183 °N, 106.057013 °W
Mullen Fire: 41.098490 °N, 106.327365 °W

Figure 1. Study areas in Colorado and Wyoming. The three burn areas (Mullen, Cameron Peak, and East Troublesome Fires) are filled in according to their burn severity (dNBR—differential normalized burn ratio): red—high severity; white—low severity; blue—unburned.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 2. STUDY AREA INFORMATION BY WILDFIRE

Information	Cameron Peak Fire	East Troublesome Fire	Mullen Fire
State/counties affected	Colorado/Larimer	Colorado/Grand, Larimer	Colorado/Jackson, Wyoming/ Carbon, Laramie
Coordinates of fire center	40.641731°N, 105.674679°W	40.228183°N, 106.057013°W	41.098490°N, 106.327365°W
Area within burn perimeter (acres)	208,913	193,812	176,878
Active burn dates	13 August 2020– 2 December 2020	14 October 2020– 30 November 2020	17 September 2020– 4 January 2021
Satellite-visible beaver dams (no.)	99	512	926
Date(s) of imagery used to map beaver dams	August 2019	August 2019	September 2014 and June 2021
SPEI drought severity in month prior to fire	South Platte Hydrologic Region: –1.80, severe drought	Colorado Headwaters Hydrologic Region: –0.95, mild drought	North Platte Hydrologic Region: –2.02, extreme drought
SPEI drought severity in hydrologic year 2019–2020	South Platte Hydrologic Region: –1.11, moderate drought	Colorado Headwaters Hydrologic Region: –1.69, severe drought	North Platte Hydrologic Region: –0.91, mild drought
Dominant 2019 NLCD land cover	Evergreen forest	Evergreen forest	Evergreen forest

Notes: SPEI—standardized precipitation evapotranspiration index; NLCD—National Land Cover Database (Dewitz and USGS, 2021).

3.1. Identification of Beaver Dams

We identified and quantified beaver dams to show actual presence and density of habitats created by beavers in the study areas. At least three individuals identified and traced beaver dams manually using publicly available high-resolution optical imagery accessed via Google Earth Pro (Google, 2022). This imagery is typically sourced either from Maxar Technologies or Airbus. The lead beaver dam mapper had manually cataloged thousands of beaver dams in aerial imagery and ground-truthed hundreds before this study. Secondary dam mappers each had formal training by the lead mapper to find and identify beaver dams, canals, and ponds, and they had manually cataloged hundreds of beaver dams in aerial imagery and ground-truthed dams before this study. When disagreement occurred on whether a feature was a beaver dam, the secondary mappers consulted the lead mapper toward consensus. Once all mappers agreed on identifications of beaver dams, the traces were exported as a multipart polyline shapefile for further landscape area classification and burn severity analysis in ESRI ArcGIS Pro (ESRI, 2022).

3.2. BRAT Classification of Current and Historic Riverscape Beaver Dam Capacity

The capacity of a riverscape to support beaver dam building (beaver dam capacity) is a quantification of the number of beaver dams that a given channel reach could support given its geomorphic, hydrologic, and ecological conditions. Riverscapes that cannot support any beaver dams tend to be waterways that are very steep, very narrow, or very degraded, or those that do not contain any wetland or riparian-adapted vegetation (e.g., willow, cottonwood, herbaceous wetland plants). Riverscapes that can support many beaver dams tend to be well vegetated. They also typically have perennial water, lower gradients, and more connected floodplains. The characteristics of riverscapes with high beaver dam capacity overlap significantly with the characteristics of fire refugia. For this reason, we consider a riverscape's beaver dam capacity to be a proxy for its baseline fire refugia potential.

To quantify beaver dam capacity, we used the Beaver Restoration Assessment Tool (BRAT). This is the most widely tested and proven tool for estimating beaver dam capacity of riverscapes in the American West. BRAT is typically run using nationally available geospatial data: LANDFIRE vegetation rasters (current/existing vegetation and historic/biophysical settings, https://landfire.gov/vegetation.php), digital elevation models from the National Elevation Data set, and hydrology/hydrography from the National Hydrography Data set (USGS, 2019). These data sets are used to quantify vegetation suitability within riverscapes, channel gradient, and low- and high-flow hydrology as variables, which then are used to estimate the maximum number of beaver dams per kilometer a given reach could theoretically sustain. Modeled estimates of beaver dam capacity were calculated via a fuzzy inference system model along a spatially explicit network and reported on a continuous scale, as well as by category, which are described in Table 3.

3.3. Burn Severity Data

3.3.1. Normalized Burn Ratio and Differential Normalized Burn Ratio Burn Severity Analysis

Variations in normalized burn ratio (NBR) and dNBR were estimated using quantitative burn severity data from the Monitoring Trends in Burn Severity database (MTBS, https://www.mtbs

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 3. BEAVER RESTORATION ASSESSMENT TOOL (BRAT) BEAVER DAM CAPACITY AND CATEGORICAL CLASSIFICATIONS

Beaver dam capacity (dams/km)	Capacity category
0	None
>0–1	Rare
>1–5	Occasional
>5–15	Frequent
>15–40	Pervasive

.gov/). This database contains analyses by the U.S. Geological Survey Center for Earth Resources Observation and Science (EROS) and the U.S. Department of Agriculture Forest Service Geospatial Technology and Applications Center (GTAC). The Bureau of Land Management Land and Resources Project Office, as part of the National Integrated Land System (NILS; Eidenshink et al., 2007), compiled the data. Landsat 8 satellite imagery (16 d return interval) was used to determine the NBR (Eq. 1) and dNBR (Eq. 2) at 30 m pixel resolution in all three of the fire perimeters (Finco et al., 2012; Miller and Thode, 2007; Roy et al., 2014):

$$\mathrm{NBR} = (\mathrm{NIR} - \mathrm{SWIR})/(\mathrm{NIR} + \mathrm{SWIR}), \quad (1)$$

$$\mathrm{dNBR} = \mathrm{NBR}_{\mathrm{prefire}} - \mathrm{NBR}_{\mathrm{postfire}}. \quad (2)$$

The NBR takes advantage of the strong differences in the way in which healthy vegetation and burnt areas reflect near-infrared (NIR) and shortwave infrared light (SWIR) (Ji et al., 2011; Pleniou and Koutsias, 2013). Healthy vegetation reflects NIR strongly, while burnt areas absorb NIR light. Conversely, healthy vegetation absorbs SWIR, while burnt areas reflect SWIR light. The NBR is a standard-form spectral index used to differentiate between these landscape conditions.

Cloud-free imagery is required in the NBR calculations to ensure high-quality data and full coverage. Image dates were chosen to ensure consistent day-of-year timing of imagery in the prefire and postfire data, as well as to keep the day-of-year timing of the prefire image as close as possible to the fire ignition date without including cloud cover, smoke interference, or other nonfire disturbance artifacts. In the Cameron Peak Fire, the prefire Landsat scene utilized was from 15 September 2018, and the postfire Landsat scene was from 7 September 2021. In the East Troublesome Fire, the prefire Landsat scene utilized was from 4 September 2020, and the postfire Landsat scene was from 7 September 2021. In the Mullen Fire, the prefire Landsat scene utilized was from 4 September 2020, and the postfire Landsat scene was from 29 August 2021. The prefire and postfire NBR values, once calculated, were then used to calculate the dNBR values.

Burn severity was classified according to the dNBR values obtained from the Landsat 8 satellite imagery (Table 4; Keeley, 2009). Fire refugia are often defined as areas where the landscape is unburned or areas that only experience low burn severity (Meddens et al., 2018; Morelli et al., 2016). Moderate burn severity is associated with variable effects on overstory vegetation and a significant amount of vegetation loss (30%–80% killed). Some soil burning may occur at this level of severity. High burn severity is associated with large-scale vegetation loss (>80% killed) and extensive soil burning.

In some burn classification schemes and maps, such as those produced by many Burned Area Emergency Response (BAER) teams, the threshold for "high severity" burning starts at 440, "moderate–high severity" is included under "high severity," and "moderate–low severity" burn classification is referred to as "moderate severity." Enhanced regrowth is often interpreted as evidence that an herbaceous ecosystem benefited from low-intensity burning and regrew robustly postfire. It can also be more generally interpreted as an area that simply had more and healthier vegetation postfire than it did prefire, and this may or may not be due to fire effects in the ecosystem. In this study, when data are reported as quantitative distributions, they adhere to the more fine-grained classifications from Table 4. When reported as categorical classification, we used a threshold of dNBR = 440 as the cutoff for high severity. Our approach did not distinguish between high and low enhanced regrowth.

Before analysis, we assessed spatial autocorrelation within the fire perimeters by estimating Moran's *I* value in 3 km × 3 km reference frames, where each pixel is represented by a unique sample point (Moran, 1950). The spatial autocorrelation in burn severity was high at the scale of the data resolution (sill [upper asymptote in the semivariogram] occurred at ~30 m), so point samples used in later analyses were spaced at a minimum of three 30 m pixels apart to ensure independent data. Statistical comparisons in burn severity and estimation of confidence intervals were conducted between beaver-dammed areas and areas without beaver dams using both Welch's two-sample *t*-test and analysis of variance (ANOVA) plus post-hoc Tukey tests (Girden, 1992; Ruxton and Beauchamp, 2008; Welch, 1947).

3.3.2. False-Color Mapping

We accessed false-color (infrared [IR], red, green) and false-color urban (SWIR1, SWIR2, red) imagery from Sentinel-2 (5 d return interval) and used it to qualitatively assess the dNBR burn severity data as the second line of evidence in this study (Drusch et al., 2012). Sentinel-2 has 10 m pixel resolution in the IR, red,

TABLE 4. BURN SEVERITY CLASSIFICATION BY DIFFERENTIAL NORMALIZED BURN RATIO (dNBR) RANGE

Burn severity classification	dNBR range ($\times 10^3$)
Enhanced regrowth postfire (high)	–500 to –251
Enhanced regrowth postfire (low)	–250 to –101
Unburned	–100 to 99
Low severity	100 to 269
Moderate–low severity	270 to 439
Moderate–high severity	440 to 659
High severity	660 to 1300

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

and green bands and 20 m pixel resolution in SWIR1 and SWIR2. We inspected all patches of fire refugia identified via dNBR analyses in cloud-free, snow-free false-color and false-color urban imagery as close to the burn date as possible. All three fires were blanketed with snow toward the end of their burn windows, so, occasionally, the closest date of cloud-free, snow-free imagery was immediately after snowmelt in spring 2021. Because minimal vegetation regrowth is expected while the landscape is under snow, images acquired immediately after snowmelt had minimal new vegetation that would obscure the patterns of burning and refugia that occurred in fall 2020 when the fires were active.

The dNBR burn severity was relatively coarse (30 m resolution) compared to the Sentinel-2 false-color imagery (10 to 20 m resolution). Burn severity calculations could also be sensitive to the scene dates used and amount of time elapsed on either side of the burn window between the scene data and the period of active burning. The false-color imagery, on the other hand, was viewable in near real-time during and immediately after burning occurred and could provide more insight into burn patterns, particularly for determining whether areas classified as enhanced regrowth experienced beneficial low-severity burning during the fire (Addabbo et al., 2016; Roy et al., 2019). Visual inspection of the false-color imagery throughout the burn perimeters created a second line of evidence to ensure that the burn severity of data points was correctly estimated and interpreted.

3.3.3. High-Resolution Optical Satellite Imagery and Field Visits

Inspection of the visible optical satellite imagery or field studies in places where the Landsat data may underperform (e.g., narrow riparian areas in steep-walled canyons or anywhere where significant time elapsed between the end of the burn and the collection of satellite data) created a third line of evidence to ensure that data points were not misclassified as burned or as fire refugia. All three fires had some postfire, high-resolution optical imagery collected by Maxar Technologies and made publicly available via Google Earth Pro. Burned (black) and unburned areas (green) could be readily visually identified in this imagery, which we used as part of our third line of evidence. The coverage of this imagery within the fire perimeters was not complete due to both smoke/cloud cover and limited data availability. Where it was available, dNBR burn severity rasters were overlaid on the optical imagery, and then the alignment between dNBR burn severity and visually observed extent of burning was visually assessed; i.e., we visually determined whether the low-severity burned areas and unburned areas as determined by dNBR were located in the same location as places that contained green vegetation in the optical imagery. The dNBR burn severity was relatively coarse (30 m resolution) compared to the optical imagery (15 to 30 cm resolution), so using the optical imagery allowed a finer-grained examination of burning patterns. We made three on-ground visits to two beaver complexes within the Cameron Peak Fire perimeter in May 2021, September 2021, and May 2022 for on-site verification of burn severity. These locations were chosen as case studies because we could observe the landscape's ecological condition and recovery postfire and for use as context when interpreting remotely sensed data collected multiple months or years after the burn period.

3.4. Sampling Scheme

We considered dNBR values from three broad landscape types: sections of riverscapes without beaver dams (n = 13,275 sample areas); sections of riverscapes with beaver dams (n = 658 sample areas); and a random sample of points outside of the riverscapes spaced a minimum of 90 m (3 pixels) apart from each other (n = 25,774 pixels). To identify riverscapes, we extracted the valley bottom area, or potential channel migration zone between two confining valley walls, along the river networks using the Valley Bottom Extraction Tool (VBET; Gilbert et al., 2016). VBET uses topographic evidence to identify valley bottoms by transforming slope and height above drainage network values into likelihoods of being valley bottom using functions that vary based on stream size. VBET additionally breaks the delineated valley bottom into segments of a uniform length, creating discrete polygons that can be used as a sampling frame (i.e., portions of riverscape with dams and portions without). In this application, each riverscape sampling polygon consisted of 100 m of valley bottom length. Though all wildfires have some degree of spatial autocorrelation in the burn severity data, the effects of it are often weak compared to the fire effects driven by landscape treatments (Chou et al., 1993; van Mantgem and Schwilk, 2009), as represented by riverscape restoration via beaver ecosystem engineering in this study. By including all riverscape areas (i.e., all of the sampling polygons) in this analysis and taking the average value of pixels within each polygon, we further reduced the influence of small-scale spatial autocorrelation within the riverscapes in the dNBR data. Random point samples outside of the riverscapes were generated within the ESRI ArcGIS Pro software using the Create-Random-Points geoprocessing tool. The spacing of the random points was three times the threshold spatial autocorrelation distance determined with Moran's I to ensure that samples were independent of each other. Figure 2 illustrates the overall sampling strategy.

The current and historic BRAT beaver dam capacity data were recorded for each riverscape sample polygon. We extracted the individual pixel dNBR value at each random point outside of the riverscapes. We calculated the average dNBR of all pixels contained within each riverscape sample area. The presence or absence of beaver dams was recorded for each sample area using the Intersect tool, and the Distance-to-Nearest-Hub in QGIS determined the distance to the nearest beaver dam from the centroid of each sample area (QGIS.org, 2022).

3.5. Evaluation of Spatial Data Structure

To explore the relationship between reach- and riverscape-scale features and burn severity, we modeled dNBR as a function

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

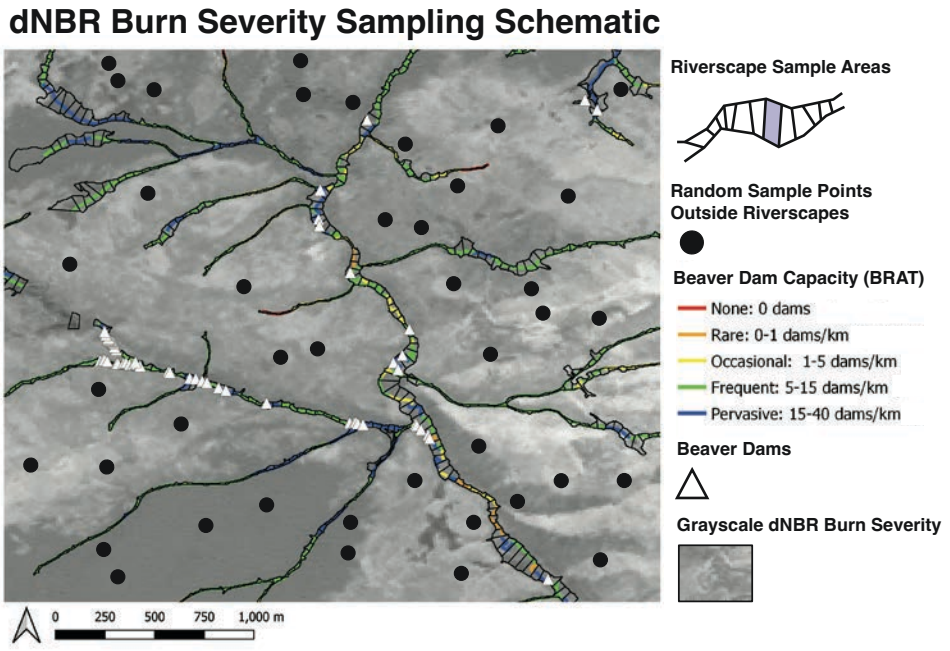


Figure 2. Example of the sampling strategy used for differential normalized burn ratio (dNBR) data collection. Valley bottom sample polygons are enclosed with thin black polygons, beaver dam capacity as modeled by Beaver Restoration Assessment Tool (BRAT) is color coded according to dam capacity category, and actual observed beaver dams are denoted with white triangles. Riverscape samples with and without beaver dams average all pixels within a given sample polygon. Random point samples were taken from outside of the riverscapes. Lat/Long: 40.263359°N, 106.046930°W.

of reach-scale beaver dam presence, the predicted habitat suitability for beaver dam building, and the spatial occurrence of beaver dams across the burned watersheds. We parameterized the effects of riverscape covariates using generalized additive model (GAM) smoothers fit using the R package mgcv (Wood, 2018). We included interactions with the "by" function. We used smoothers and interactions to account for spatial patterns in riverscape covariates and for nonlinear relationships between reach and riverscape covariates. We fit simple GAMs to the data where dNBR was predicted by a spline smoother (s) on the interaction between the BRAT dam capacity and the distance to the nearest beaver dam using the restricted maximum likelihood method (Eq. 3):

$$\text{dNBR} \sim \text{BRAT category} + s(\text{distance to nearest dam}, \text{by} = \text{BRAT category}). \quad (3)$$

4. RESULTS

4.1. Differential Normalized Burn Ratio (dNBR) Burn Severity of Fires Overall and by Landscape Type

When evaluating the entire population of burn severity samples (n = 39,707), the bulk of the data ranged between low-severity and moderate–high-severity burns in each of the three study fires (Fig. 3).

This distribution of burn severity is commonly observed in megafires, though on its own, it does not give a clear picture of how the fire impacted the different parts of the landscape until stratified by landscape category: outside of riverscapes, riverscapes without beaver dams, and riverscapes with beaver dams (Fig. 4). The high-resolution imagery beaver dam mapping determined that the Cameron Peak Fire had 99 satellite-visible beaver dams, the East Troublesome Fire had 512 satellite-visible beaver dams, and the Mullen Fire had 926 satellite-visible beaver dams.

The population of burn severity samples outside of the river network and away from beaver-dammed areas (n = 25,774) had a roughly bimodal distribution. One peak was in the low-severity to unburned range, and a second peak was in the moderate–high-severity range (Fig. 4, top row). This shape of data distribution is reflective of the overall pattern of fire effects observed in the dNBR burn severity maps (Fig. 1). Many large patches of moderate- and high-severity burning intermingled with several small to midsized patches of low-intensity or unburned landscape, where often either alpine meadows with few trees were present or protected human infrastructure (roads, towns, housing developments, properties with cleared timber, etc.) was present.

In the population of burn severity samples that were in riverscapes without beaver dams (n = 13,275), the data from the Cameron Peak Fire had a roughly bimodal distribution. One peak was in the low-severity to unburned range, and a second peak appeared in the moderate–high-severity range (Fig. 4, middle row, left column). The data from the East Troublesome and Mullen Fires had a right-skewed distribution with a single peak in the low-severity to unburned range and then a thick tail extending out into the high-severity range (Fig. 4, middle row, middle and right columns).

When evaluating the population of burn severity samples within beaver-dammed areas (n = 658), the data from all three

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

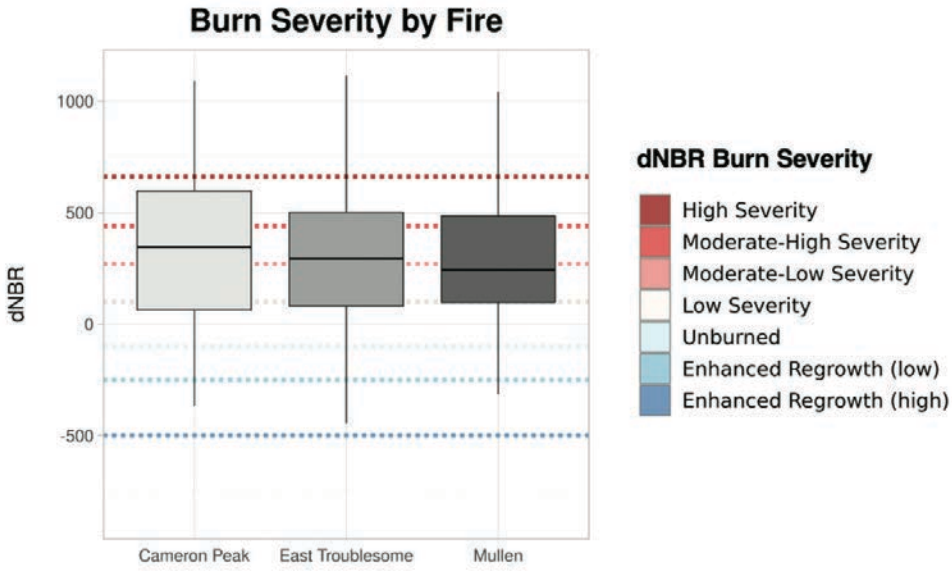


Figure 3. Distribution of sample differential normalized burn ratio (dNBR) burn severity by fire. Color-coded dashed lines are the lower thresholds of the burn severity classifications. Low-severity burning or less is considered fire refugia.

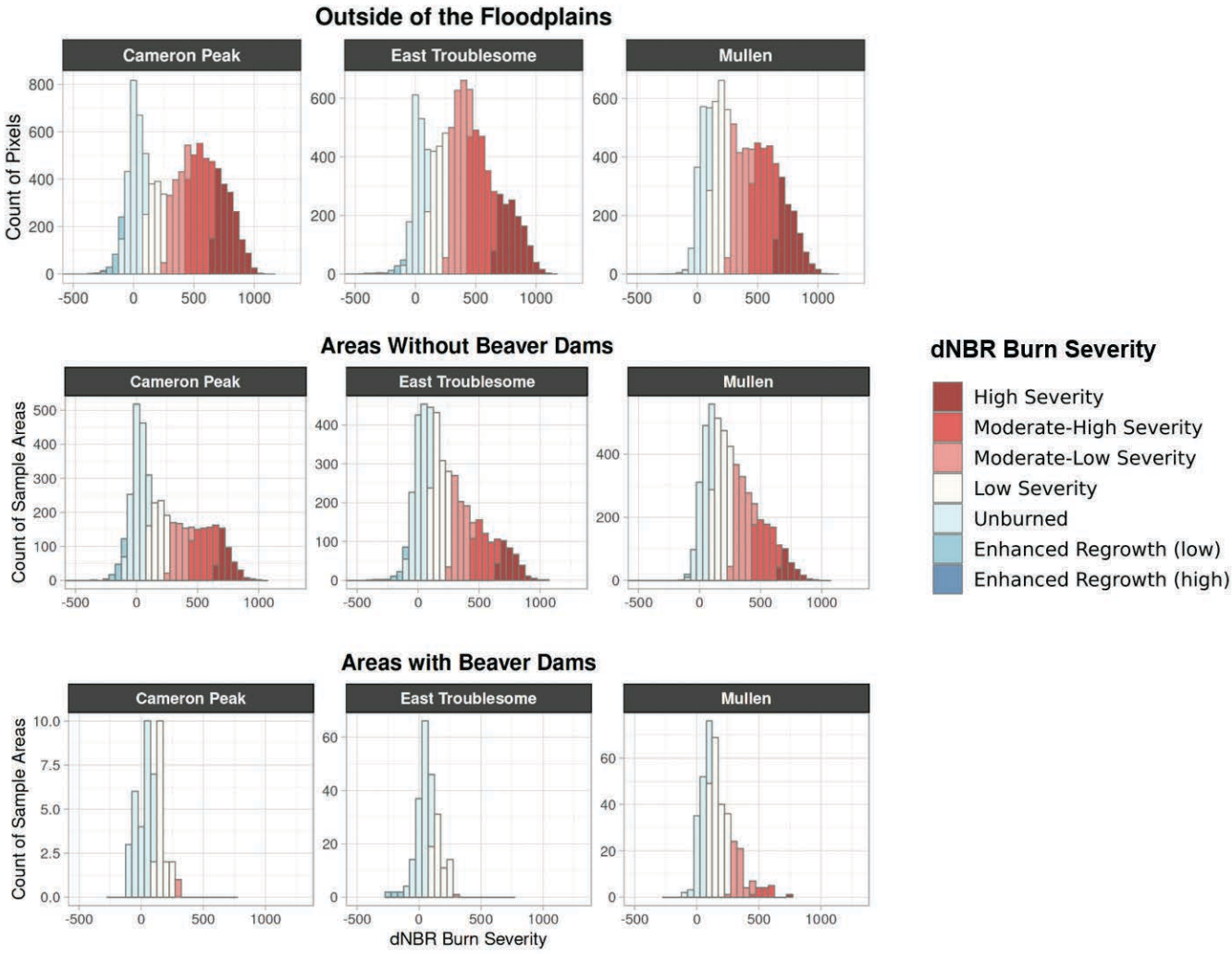


Figure 4. Distribution of sample differential normalized burn ratio (dNBR) burn severity by fire and landscape type.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 5. MEAN BURN SEVERITY BY FIRE AND LANDSCAPE TYPE

Landscape type	Cameron Peak Fire	East Troublesome Fire	Mullen Fire
Outside of the riverscapes	378 (M) *n* = 9332 pixels	369 (M) *n* = 8480 pixels	330 (M) *n* = 7961 pixels
Riverscapes without beaver dams	251 (L) *n* = 4002 sample areas	242 (L) *n* = 4303 sample areas	266 (L) *n* = 4970 sample areas
Riverscapes with beaver dams	72 (U) *n* = 45 sample areas	70 (U) *n* = 230 sample areas	167 (L) *n* = 383 sample areas

Notes: U—unburned; L—low severity; M—moderate severity; *n*—count of pixels or sample areas included.

fires had a roughly symmetric distribution around a sharp peak in the unburned range, with a slight right-skew and a short tail extending out into the moderate-severity range (Fig. 4, bottom row). These data distributions demonstrate that the majority of the landscape within the beaver-dammed areas was unburned or experienced low-severity burning, meeting the definition of fire refugia. The differences in burn severity data by landscape type (riverscapes with beaver dams, riverscapes without beavers, and outside of the riverscapes) were reflected in the mean burn severity values for each fire included in this study (Table 5).

The differences between the landscape types were statistically significant ($p < 0.05$) using both Welch's two-sample *t*-test and the ANOVA plus post-hoc Tukey tests (Girden, 1992; Ruxton and Beauchamp, 2008; Welch, 1947). Significant differences in burn severity were found within each fire and in all the fire data combined. The beaver dammed riverscapes experienced significantly less severe burning than the riverscapes without beavers and the areas outside of the riverscapes by a large margin (measured dNBR differences ranged from −99 to −306). The riverscapes without beavers experienced significantly less severe burning than the areas outside of the riverscapes by a smaller margin (measured dNBR differences ranged from −64 to −127).

4.2. Fire Refugia Area in Riverscapes

To further explore the potential ecological and human value of riverscapes as fire refugia, we calculated the total floodplain area that fell into each burn intensity classification in riverscapes with and without beaver dams (Table 6). Fire refugia were present in riverscapes with and without beavers. Beaver dams are relatively rare landscape features compared to riverscapes without beavers, so beaver-dammed riverscapes only constituted ~15% of total riverscape fire refugia by area. However, 89% of beaver-dammed riverscapes were classified as fire refugia compared to only 60% of riverscapes without beaver dams. The proportion of beaver-dammed riverscapes that were fire refugia was higher than the proportion of riverscapes without beaver that were fire refugia, so beaver-dammed riverscapes are more reliable fire refugia.

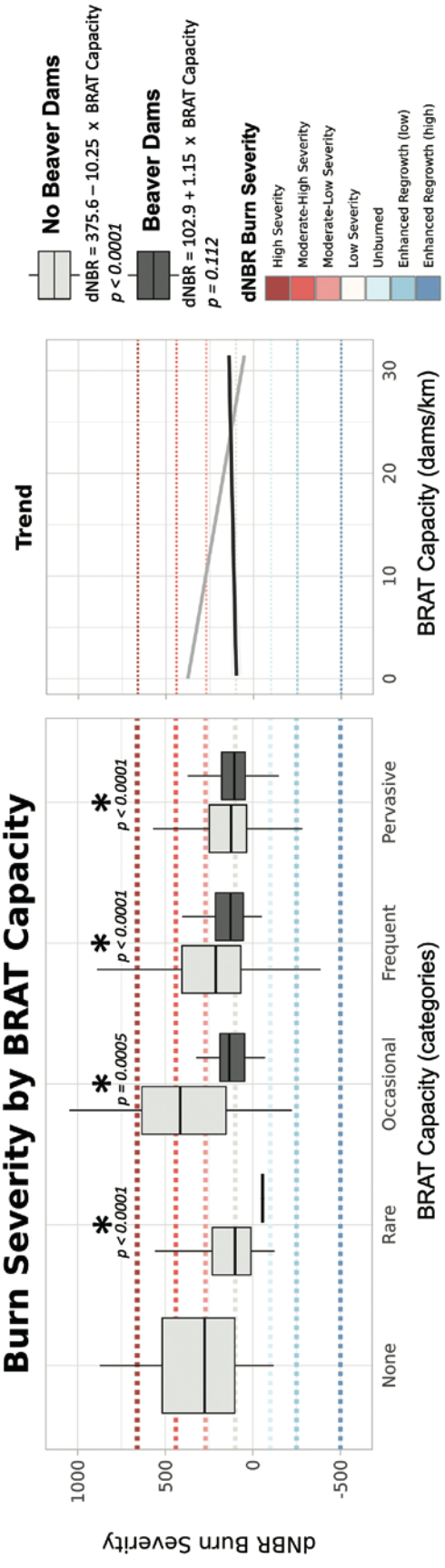
4.3. Beaver Dam Capacity as a Proxy for Riverscape Fire Refugia Potential

We compared burn severity across each BRAT beaver dam capacity category as well as within each category according to whether the sample area had beaver dams (Fig. 5).

TABLE 6. FLOODPLAIN AREA WITHIN EACH BURN CLASSIFICATION

Riverscapes with beaver dams			
Burn category		**Area (km²)**	**Portion of area (%)**
Unburned or enhanced regrowth		6.58	46
Low intensity		4.65	43
Moderate intensity		1.3	9
High intensity		0.57	2
	Total	*13.1*	*100.00*
Riverscapes without beaver dams			
Burn category		**Area (km²)**	**Portion of area (%)**
Unburned or enhanced regrowth		37.18	32
Low intensity		28.38	27.5
Moderate intensity		16.71	17.5
High intensity		14.32	23
	Total	*96.59*	*100.00*
Amount of fire refugia (burn severity of low, unburned, or enhanced regrowth)			
Riverscape type		**Area (km²)**	**Portion of area (%)**
Riverscapes with beaver dams		11.23	89
Riverscapes without beaver dams		65.56	60

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user



Beaver-modified riverscapes had significantly ($p < 0.001$) lower burn severities than riverscapes without beaver dams within each BRAT dam capacity category (Fig. 5). Table 7 reports average dNBR values, calculated differences in dNBR, and the 95% confidence interval for the estimated difference in means from the Welch's *t*-tests. These results suggest that the presence of beaver dams lowers burn severity in all types of riverscapes, including those that already have many characteristics of good beaver habitat and fire refugia potential (e.g., perennial water, riparian vegetation, channel complexity). Simple linear models of burn severity as a function of BRAT capacity were created from the dammed and undammed riverscape data sets. The linear model fit to the undammed riverscape data set was statistically significant ($p < 0.0001$) with a negative slope (i.e., higher beaver dam capacity → lower burn severity). The linear model fit to the beaver-dammed riverscape data set was not statistically significant ($p = 0.112$).

Within the beaver-modified riverscapes, no significant differences existed in dNBR between the riverscape beaver dam capacity categories when tested with ANOVA and post-hoc Tukey tests (pairwise p values in Table 8). The ANOVA test in beaver-dammed areas had an overall F value of 1.93 and p value of 0.123. Sample size in the "rare" category within beaver-dammed riverscapes was small ($n = 2$), so we report the differences here with the caveat that the statistical significance of those differences should be interpreted with caution. In the riverscapes without beaver dams, all BRAT dam capacity categories were significantly different from one another, except "rare × pervasive," which were not significantly different (pairwise p values in Table 8). The ANOVA test in areas without beavers had an overall F value of 540.2 and a p value < 0.0001. The largest difference in burn severity between beaver-dammed riverscapes and riverscapes without beavers occurred in places that fell into the "occasional" dam capacity category.

4.4. Effects of Distance to Nearest Beaver Dam

The GAM-based evaluation of spatial structure in the burn severity data revealed moderate underlying spatial relationships between beaver dam (and beaver dam potential) and burn severity. The model (Eq. 3) explained 23.9% of the overall variance in

Figure 5. (Left) Distribution of sample differential normalized burn ratio (dNBR) burn severity by Beaver Restoration Assessment Tool (BRAT) capacity categories with and without beaver damming. All differences between beaver-dammed riverscapes and riverscapes without beaver dams marked with an asterisk were statistically significant ($p < 0.05$) using Welch's two sample *t*-tests and analysis of variance (ANOVA) plus post-hoc Tukey tests. Test statistic information is labeled on the plot above. There were no beaver-dammed riverscapes in the "none" category. (Right) Trend in burn severity with increasing BRAT capacity with and without beaver dams. Both metrics are shown on a continuous scale with the equations and significance values labeled on the figure above.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 7. AVERAGE DIFFERENTIAL NORMALIZED BURN RATIO (dNBR) BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) CAPACITY

BRAT capacity category	Beaver dNBR	Beaver burn category	No-Beaver dNBR	No-Beaver burn category	Difference in dNBR (Beaver – No Beaver)	Welch *t*-test statistics
None	N/A *n* = 0	N/A	313 *n* = 437	Moderate	N/A	N/A
Rare	–56 *n* = 2	Unburned	155 *n* = 142	Low	–211	*t* = –11.266 *p* < 0.0001 CI: (–250, –170)
Occasional	131 *n* = 8	Low	398 *n* = 2844	Moderate	–267	*t* = –5.8 *p* = 0.0005 CI: (–374, –159)
Frequent	140 *n* = 137	Low	250 *n* = 6042	Low	–109	*t* = –10.2 *p* < 0.0001 CI: (–131, –88)
Pervasive	125 *n* = 523	Low	150 *n* = 3798	Low	–25	*t* = –4.1 *p* < 0.0001 CI: (–37, –13)

Notes: N/A—not applicable; CI—confidence interval; *n*—number of reaches.

dNBR values as a function of proximity to beaver dams, when allowing for separate interaction smooth by predicted beaver dam capacity. Visualization of the smooth functions by riverscape dam capacity (Fig. 6) detected a clear effect of proximity to beaver dams in the "rare," "occasional," and "frequent" dam capacity categories but not in the "none" or "pervasive" categories. The proximity effect began to plateau around 1000–1500 m from a beaver dam in the "rare" and "frequent" categories, and around 2000 m in the "occasional" category.

The best-fit model stabilized around a basis size (*k*) of 50 using thin-plate splines (Table 9). We tested basis sizes up to 100 but did not observe meaningful changes in test statistics with further increases in basis size beyond 50. This, in addition to the effective degrees of freedom for each smoothing term being significantly lower than the basis size, suggests that the basis size is appropriate for this data set (Pedersen et al., 2019).

TABLE 8. PAIRWISE SIGNIFICANCE OF BURN SEVERITIES WITHIN RIVERSCAPE TYPE BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) CATEGORY

Beaver-dammed riverscapes	
Occasional × Rare	*p* = 0.2373261 (small sample size)
Frequent × Rare	*p* = 0.1282717 (small sample size)
Pervasive × Rare	*p* = 0.1778316 (small sample size)
Frequent × Occasional	*p* = 0.9974858
Pervasive × Occasional	*p* = 0.9991081
Pervasive × Frequent	*p* = 0.6068951
Riverscapes without beavers	
Rare × None	*p* < 0.0001
Occasional × None	*p* < 0.0001
Frequent × None	*p* < 0.0001
Pervasive × None	*p* < 0.0001
Occasional × Rare	*p* < 0.0001
Frequent × Rare	*p* < 0.0001
Pervasive × Rare	*p* = 0.9991153
Frequent × Occasional	*p* < 0.0001
Pervasive × Occasional	*p* < 0.0001
Pervasive × Frequent	*p* < 0.0001

4.5. Qualitative Burn Severity Observations

4.5.1. False-Color Mapping

No significant disagreements were detected between the fire refugia observed in false-color imagery (false-color and false-color urban; Fig. 7) and the measured dNBR burn severity that indicated fire refugia. The higher-resolution imagery from Sentinel-2

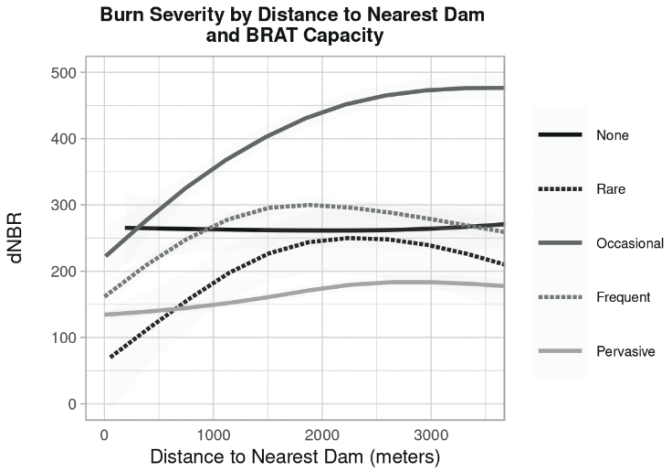


Figure 6. Generalized additive model (GAM) smoothing functions for differential normalized burn ratio (dNBR) as a function of distance to nearest beaver dam, separated by Beaver Restoration Assessment Tool (BRAT) riverscape dam capacity categories.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

TABLE 9. GENERALIZED ADDITIVE MODEL (GAM) STATISTICS AS A FUNCTION OF DISTANCE TO NEAREST BEAVER DAM, SEPARATED BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) RIVERSCAPE DAM CAPACITY CATEGORIES

Smoothing function	Effective degrees of freedom	*P* value
Dam distance : BRAT-None	12.40	$p < 0.0001$
Dam distance : BRAT-Rare	5.41	$p = 0.00639$
Dam distance : BRAT-Occasional	31.27	$p < 0.0001$
Dam distance : BRAT-Frequent	31.25	$p < 0.0001$
Dam distance : BRAT-Pervasive	9.89	$p < 0.0001$

showed the gradient of transition from moderate- and high-severity burning outside of the river network to low-severity and unburned vegetation within the beaver complexes. The fires were not simply jumping over them due to their position in the valley bottom. Some imagery showed fire burning on all sides of the beaver complexes that was still unable to burn within them (Fig. 8).

4.5.2. Visual Inspection of Aerial Photographs and Field Visits

The fire refugia found in beaver complexes was clearly visible both in high-resolution satellite imagery (Fig. 9) and during field visits (Fig. 10). These visually identified fire refugia aligned with the dNBR identified fire refugia in all three fires. In the Mullen Fire, some very narrow ribbons of fire refugia in the riparian zone were visually identified as being unburned but appeared as low burn severity in the dNBR data. This result was likely due to the size of the dNBR pixels being on the same order as the width of the riparian corridor, so the influence of pixels containing both riparian and hillslope landscape was disproportionately large. Based on this, the points within the beaver-dammed areas in the Mullen Fire may be biased toward higher dNBR values and burn severity classes. This bias happened with relative frequency in the Mullen Fire, but we did not observe it in the other fire areas. We were also able to observe the gradient of burn severity on-site that was noted in the false-color mapping observations (Fig. 9, bottom).

5. DISCUSSION

5.1. Beaver Complexes as Uniquely Fire-Resistant Landscape Features

The majority of riverscapes are fire refugia, but riverscapes without beaver dams are significantly less reliable fire refugia

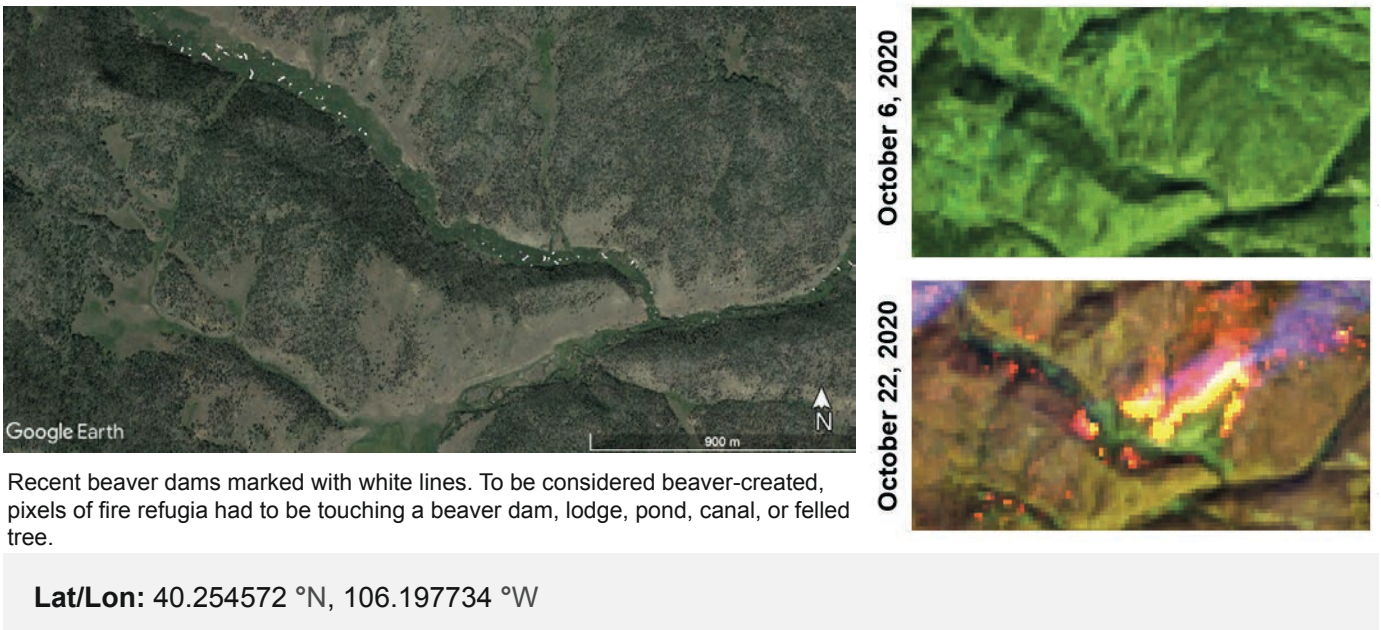


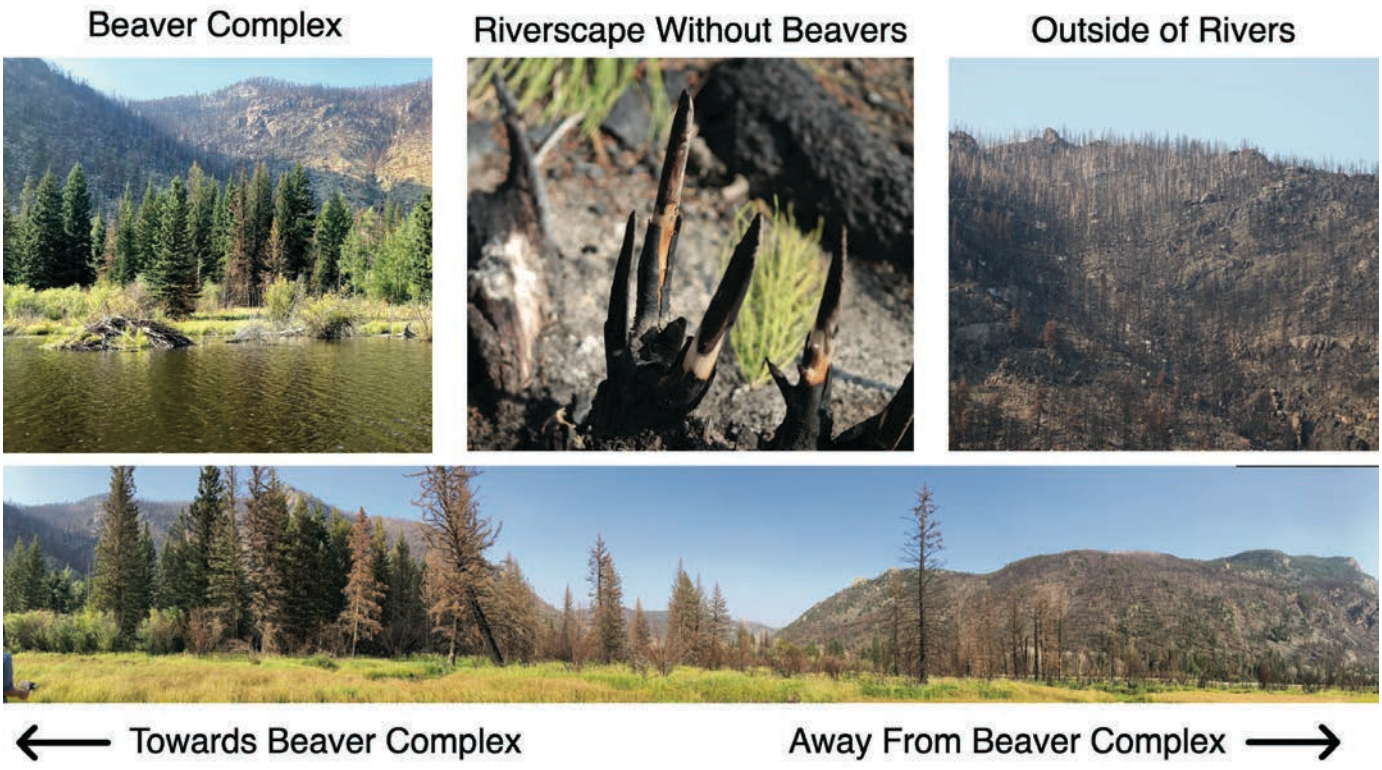
Figure 7. Example of qualitative assessment of burn severity within the fire perimeters using false-color mapping (green—unburnt vegetation, dark orange—burnt vegetation, bright orange and yellow—hot spots). Left: Satellite image of beaver complexes highlighted with semitransparent white polygons. Right top: Example of a false-color image immediately prior to the fire to assess prefire conditions. Right bottom: Example of a false-color image as close to the date of the fire as possible to assess postfire conditions.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user



Lat/Lon: 41.111878 °N, 106.379883 °W

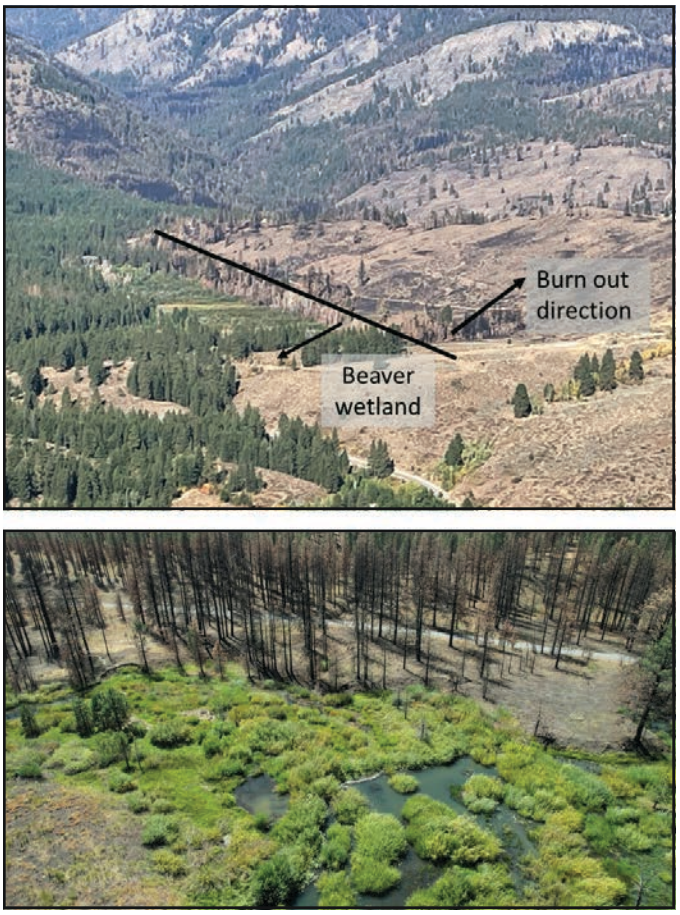
Figure 8. Example of qualitative assessment of burn severity within the fire perimeters using true-color aerial and satellite imagery. Left: Landscape with beaver damming before the fire. Middle: Landscape with beaver damming after the fire where the beaver complexes are the only green left. Right: Differential normalized burn ratio (dNBR) burn severity raster overlain on top of the landscape showing the alignment between observed greenness and low burn severity around beaver dams (traced with black lines). 1000 ft = ~305 m.



Lat/Lon: 40.705101 °N, 105.757766 °W

Figure 9. Example of qualitative assessment of burn severity within the fire burn perimeters through field visits and on-site photography. Top left: Beaver complex after the fire with intact, mature vegetation. Top middle: Willow burnt to stumps after the fire in the river network outside of the beaver complex. Top right: Hillslopes surrounding the beaver complex with high-severity burning and total vegetation loss. Bottom: Panoramic photo of the landscape observing the gradient of burn severity changing with increased distance from the beaver complex.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user



Top: 48.476770 °N, 120.256867 °W
Bottom: 39.957443 °N, 120.212691 °W

Figure 10. (Top) Example of a beaver complex assisting in our human wildfire management activities. The beaver complex provided a safe point from which to backburn to reduce fuel loads near Sun Mountain Lodge, Winthrop, Washington, 2021 (photo credit: Kamansky 2021). (Bottom) Example of a small patch of beaver-created fire refugia from the 2021 Beckworth Fire in California.

(60% refugia) than riverscapes with beaver dams (89% refugia). This finding supports H1, which hypothesized that riverscapes have lower burn severity than the rest of the landscape. Additionally, the beaver-modified riverscapes were significantly more resistant to burning during megafire than either the nondammed riverscapes or the nonriverine areas. This result supports H2, which hypothesized that beaver-dammed riverscapes have lower burn severity than riverscapes without beaver dams. This was true in all three fires individually and aggregated, as well as across all modeled beaver dam capacity categories. The relationships between burn severity and actual beaver damming, riverscape beaver dam capacity, and historic riverscape beaver dam capacity were nonlinear. A significant decreasing trend in burn severity was found in riverscapes without beaver dams as the dam capacity increased. However, there was consistently low burn severity with no directional trend associated with dam capacity in riverscapes with beaver dams. This outcome only partially supports H3, which hypothesized that riverscapes with a higher capacity for beaver dams have lower burn severity than those with a lower capacity for beaver dams.

We had hypothesized in H3 that higher riverscape dam capacity would be associated with lower dNBR. In the case of the beaver-dammed riverscapes, all dam capacity categories had low dNBR, and no significant differences or trend existed between categories. In the case of riverscapes without beaver dams, a significant decreasing trend appeared (higher riverscape dam capacity = lower dNBR). It was not a uniform trend, however, as riverscapes with no dam capacity burned significantly less than riverscapes with a "rare" dam capacity, which may be related to the biophysical conditions in very narrow, steep, or sparsely vegetated catchments that are unsuitable for beaver occupancy and the relationship of those conditions to fire spread behaviors. The largest relative difference between the riverscapes with and without beaver dams occurred in the "occasional" dam capacity category (although sample size was low in that category at $n = 8$ sample areas) and decreased as dam capacity changed in either direction. This was the riverscape poorly represented in our data set, however, potentially influencing the magnitude of impact estimated and pointing to the need for additional attention in future work.

We determined that the distance to nearest beaver dam and current beaver dam capacity of a riverscape can explain 23.9% of the variance in burn severity data. Numerous different factors likely influence the remaining variability in burn severity in the Rocky Mountain region, including wind speed, wind direction, humidity, fuel age, fuel moisture, fuel volume, antecedent climate conditions, prior fuel treatments, and bark beetle tree kill. The consistency of resistance to fire observed in beaver-dammed areas and the magnitude of influence that beaver damming had on burn severity merit consideration in future fire management planning efforts in North America.

This study was not the first to demonstrate that beaver-dammed riverscapes are uniquely fire-resistant landscape features (Fairfax and Whittle, 2020; Foster et al., 2020; Markle et al., 2022; Weirich, 2020; Whipple, 2019; Wohl et al., 2022). It is the first to show, however, that the effect persists during the extreme wildfire behaviors common in megafires. The innate ecosystem engineering behaviors of beavers are complementary to fire risk-reduction strategies (Table 2). While this study focused on probing the upper limit of fire resistance that beaver complexes could maintain, many questions remain across the spectrum of wildfire burn severity, scale of impact, and influence of beaver-damming activity. For example, how and when can beaver-dammed riverscapes function as fire breaks? Anecdotal evidence from the 2021 Cedar Creek Fire in north-central Washington demonstrates a large beaver complex serving as a natural firebreak and a point for enacting strategic fire protection for human infrastructure. This beaver complex helped protect structures near Winthrop, Washington, by providing a safe point from which to backburn

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

to remove hazardous fuels from the oncoming wildfire path (Fig. 10, top). The ability for beaver wetlands to function as firebreaks has different potential applications in wildfire mitigation efforts than the more commonly discussed role they play in creating isolated fire-resistant patches (e.g., Fig. 10, bottom).

5.2. Potential Changes to Postfire Processes in Beaver-Supported Fire Refugia

Fire refugia are ecologically important postfire as well (Brazier et al., 2021; Meddens et al., 2018; Morelli et al., 2016). Mature vegetation can help reseed nearby burnt riparian areas more quickly postfire. It provides a distributed network of habitat patches for pollinators and seed dispersers throughout the burned areas (Andrus et al., 2021; Blomdahl et al., 2019; Downing et al., 2020; Landesmann and Morales, 2018). From a geomorphic standpoint, fire refugia patches are particularly well suited to slow incoming water and trap wildfire-mobilized sediment and nutrients, given how the redundant dam-vegetation structure of beaver-modified riverscapes reduces unit stream power by spreading the force of flow (Short et al., 2015). Expansion of beaver habitat across watersheds within their native range could prevent or reduce the severity of destructive, channel-incising debris-flow events that commonly occur after wildfires (Cluer and Thorne, 2014). For example, debris flows after wildfire can cause channel scouring and incision to bedrock (Cannon and DeGraff, 2009). These events straighten and deepen streams, removing in-channel and riparian vegetation and large wood by rapidly conveying it downstream. As a result, streams are further isolated from their floodplains, which damages the biological community within the channel. Numerous aquatic organisms cannot tolerate high suspended sediment loads and, in particular, struggle with ash that washes into the stream. Heavy loads of fine sediment in streams after wildfire can easily suffocate fish, macroinvertebrates, and amphibians by coating their respiratory organs (Bash et al., 2001; Gresswell, 1999; Rinne, 1996). The transport of high concentrations of limiting nutrients, like phosphate, with sediment after wildfire can also contribute to eutrophication in catchments downstream (Brass et al., 1996; Gresswell, 1999).

Wildfire in mixed conifer forests of western North America can stimulate regrowth of riparian deciduous shrubs that evolved with fire and regrow from their roots rapidly if not severely burned, as seen in the enhanced regrowth classification data (Schier et al., 1985; Shinneman et al., 2013; Stein et al., 1992). This rapid vegetation response can provide significant and critical food resources for beavers within a burned watershed, which may support their continued occupancy of a stream after fire or allow reestablishment where legacy human impacts such as livestock grazing had previously reduced or eliminated beaver food resources. For example, streams that have become severely incised following wildfire-induced debris-flow events but that have recovered fire-adapted riparian vegetation quickly have been targeted for beaver relocation and beaver-based restoration. These beaver translocation actions are meant to rapidly restore incision and reconnect streams to their floodplains, and they have shown encouraging success (Dittbrenner et al., 2022). Success is reflected in recent research that shows significant changes in stream channel width/depth ratio and clear reductions in phosphate transport in streams where beavers have been able to establish following severe wildfire impacts, thus increasing refugia and resilience in preparation for the next wildfire (Whipple, 2019; Pollock et al., 2014).

5.3. Study Limitations

More research is necessary to compare how other types of restored riverscapes (e.g., stage 0 restoration, non-beaver LTPBR, beaver mimicry via beaver dam analogs) respond to wildfire, and whether they create fire refugia at the same rates and as consistently as does beaver activity. Beavers are not ubiquitous, and not everywhere in the world has or had beavers controlling their waterways, and so other types of functioning, resilient riverscapes exist around the globe. Further investigation is warranted in expanding this style of analysis in future studies across fire-prone landscapes, especially in places where other types of river restoration activities affect portions of the river network within burn perimeters. Additionally, the three fires examined in this study were similar in fire and landscape characteristics, and, as such, expanded research on additional fires from a wider variety of physical and ecological settings that also include beaver damming within their perimeters would help to elucidate the sources of variability in burn severity as a function of riverscape and beaver activity state.

Given the widespread and profound influence beavers had historically in North America, it is possible that beaver presence is a requirement for full restoration in some watersheds. We know that many more beavers existed in North America historically than at present (100–400 million estimated before the industrialized fur trade and 10–40 million today; estimates from Naiman et al., 1988). Beavers were widely distributed on this continent, occupying the vast majority of watersheds from the east coast to the west coast, and from northern Mexico up into northern Canada and Alaska. The entire river network and flow of water across this continent was fundamentally different before beavers were systematically and intentionally removed from the landscape (Fouty, 2018; Wohl, 2011, 2021b). As such, it is reasonable to imagine that riverscapes without any influence of beaver activity were not as common of a phenomenon in the past (Wohl, 2021b). Thus, many historical riverscape fire refugia were likely in some way influenced by beavers.

To explore this assumption, more research is needed to model the historic population and distribution of beavers in the western United States, as well as the scale and duration of their impact on hydrologic and geomorphic riverine processes. In particular, a better understanding is necessary regarding how the activities and impacts of beavers varied over space and time when their populations and habitats were not as impacted by human activity as they are today. Beavers naturally cycle through locations as food resources wane or sediment accumulations turn

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

ponds into meadows, and local populations fluctuate with disease and predation cycles (Johnston, 2017; Gable et al., 2020). Evidence suggests that abandoned beaver dam complexes also play a significant role in riverscape processes (Ives, 1942; Polvi and Wohl, 2012; Ronnquist and Westbrook, 2021; Woo and Waddington, 1990). Abandoned complexes may continue to function as wildfire refugia, despite being unattended cyclically. Within the context of wildfire, current data are insufficient to characterize with certainty the durability of the biogeomorphic effects of beaver activity in fluvial systems during the periods when the beavers themselves are not physically present. This research, along with other recent work, does clearly demonstrate that beavers are a critical component of nature-based river restoration in North America and Eurasia, but many opportunities remain to deepen understanding of their role.

6. CONCLUSIONS

This study showed that beaver-modified riverscapes are resistant to megafire-scale disturbance. This resilience is directly attributable to beaver dam- and canal-building activity, although the geomorphic settings conducive to beaver activity also confer a degree of resilience. Therefore, even with the current degraded state of many river systems and the trajectory of increasing wildfire severity under a changing climate, beaver ecosystem engineering offers proven resilience to megafires and a reliable source of wildfire refugia for freshwater-dependent biological communities, including humans. Beaver ecosystem engineering is complementary to, not in opposition to, current fire-mitigation strategies. Beaver populations, and in turn beaver dam building, can be part of a comprehensive fire-mitigation strategy while offering additional benefits to biological communities, including humans, even when fire is not an active threat. Beaver conservation, beaver coexistence strategies, and beaver-based restoration should be strongly considered for inclusion when planning fire risk-mitigation strategies, and when developing or updating watershed and land management plans.

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation under EES grant no. 1928693.

REFERENCES CITED

Addabbo, P., Focareta, M., Marcuccio, S., Votto, C., and Ullo, S.L., 2016, Contribution of Sentinel-2 data for applications in vegetation monitoring: Acta Imeko, v. 5, no. 2, 44, https:///doi.org/10.21014/acta_imeko.v5i2.352.

Agee, J.K., 1998, The landscape ecology of western forest fire regimes: Northwest Science, v. 72, p. 24.

Andersen, D.C., and Shafroth, P.B., 2010, Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona: Ecohydrology, v. 3, no. 3, p. 325–338, https://doi.org/10.1002/eco.113.

Anderson, N.L., Paszkowski, C.A., and Hood, G.A., 2015, Linking aquatic and terrestrial environments: Can beaver canals serve as movement corridors for pond-breeding amphibians?: Animal Conservation, v. 18, p. 287–294, https://doi.org/10.1111/acv.12170.

Andrus, R.A., Martinez, A.J., Jones, G.M., and Meddens, A.J., 2021, Assessing the quality of fire refugia for wildlife habitat: Forest Ecology and Management, v. 482, https://doi.org/10.1016/j.foreco.2020.118868.

Bartelt, K., 2021, Valley Bottom Inundation Patterns in Beaver-Modified Streams: A Potential Proxy for Hydrologic Inefficiency [M.S. thesis]: Logan, Utah, Utah State University, 78 p., https://doi.org/10.26076/a66b-0708.

Bash, J., Berman, C.H., and Bolton, S., 2001, Effects of Turbidity and Suspended Solids on Salmonids: Final Research Report Research Project T1803, Task 42, prepared for Washington State Transportation Center, 92 p.

Bashinskiy, I.V., 2020, Beavers in lakes: A review of their ecosystem impact: Aquatic Ecology, v. 54, no. 4, p. 1097–1120, https://doi.org/10.1007/s10452-020-09796-4.

Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., and Pollock, M.M., 2010, Process-based principles for restoring river ecosystems: Bioscience, v. 60, no. 3, p. 209–222, https://doi.org/10.1525/bio.2010.60.3.7.

Blomdahl, E.M., Kolden, C.A., Meddens, A.J., and Lutz, J.A., 2019, The importance of small fire refugia in the central Sierra Nevada, California, USA: Forest Ecology and Management, v. 432, p. 1041–1052, https://doi.org/10.1016/j.foreco.2018.10.038.

Bowman, D.M., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., and Krawchuk, M.A., 2011, The human dimension of fire regimes on Earth: Journal of Biogeography, v. 38, no. 12, p. 2223–2236, https://doi.org/10.1111/j.1365-2699.2011.02595.x.

Brass, J.A., Ambrosia, V.G., Riggan, P.J., and Sebesta, P.D., 1996, Consequences of fire on aquatic nitrate and phosphate dynamics in Yellowstone National Park, *in* Greenlee, J.M., ed., Proceeding of the 2nd Biennial Conference on the Greater Yellowstone Ecosystem, Sep. 19–21, 1993, Yellowstone National Park: Fairfield, Washington, International Association of Wildland Fire, p. 53–57.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., and Brown, C.M.L., 2021, Beaver: Nature's ecosystem engineers: WIREs Water, v. 8, no. 1, https://doi.org/10.1002/wat2.1494.

Cannon, S.H., and DeGraff, J., 2009, The increasing wildfire and post-fire debris-flow threat in western USA, and implications for consequences of climate change, *in* Sassa, K., and Canuti, P., eds., Landslides—Disaster Risk Reduction: Berlin, Springer, p. 177–190, https://doi.org/10.1007/978-3-540-69970-5_9.

Castro, J.M., and Thorne, C.R., 2019, The stream evolution triangle: Integrating geology, hydrology, and biology: River Research and Applications, v. 35, no. 4, p. 315–326, https://doi.org/10.1002/rra.3421.

Chou, Y.H., Minnich, R.A., and Chase, R.A., 1993, Mapping probability of fire occurrence in San Jacinto Mountains, California, USA: Environmental Management, v. 17, no. 1, p. 129–140, https://doi.org/10.1007/BF02393801.

Ciotti, D.C., McKee, J., Pope, K.L., Kondolf, G.M., and Pollock, M.M., 2021, Design criteria for process-based restoration of fluvial systems: Bioscience, v. 71, no. 8, p. 831–845, https://doi.org/10.1093/biosci/biab065.

Cluer, B., and Thorne, C., 2014, A stream evolution model integrating habitat and ecosystem benefits: River Research and Applications, v. 30, no. 2, p. 135–154, https://doi.org/10.1002/rra.2631.

Coen, J.L., Stavros, E.N., and Fites-Kaufman, J.A., 2018, Deconstructing the King megafire: Ecological Applications, v. 28, no. 6, p. 1565–1580, https://doi.org/10.1002/eap.1752.

Dewitz, J., and U.S. Geological Survey, 2021, National Land Cover Database (NLCD) 2019 Products (ver. 2.0, June 2021): U.S. Geological Survey Data Release, https://doi.org/10.5066/P9KZCM54.

Dittbrenner, B.J., Pollock, M.M., Schilling, J.W., Olden, J.D., Lawler, J.J., and Torgersen, C.E., 2018, Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation: PLoS One, v. 13, no. 2, https://doi.org/10.1371/journal.pone.0192538.

Dittbrenner, B.J., Schilling, J.W., Torgersen, C.E., and Lawler, J.J., 2022, Relocated beaver can increase water storage and decrease stream temperature in headwater streams: Ecosphere, v. 13, no. 7, https://doi.org/10.1002/ecs2.4168.

Downing, W.M., Krawchuk, M.A., Coop, J.D., Meigs, G.W., Haire, S.L., Walker, R.B., Whitman, E., Chong, G., Miller, C., and Tortorelli, C., 2020, How do plant communities differ between fire refugia and fire-generated early-seral vegetation?: Journal of Vegetation Science, v. 31, no. 1, p. 26–39, https://doi.org/10.1111/jvs.12814.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., and Martimort, P., 2012, Sentinel-2: ESA's optical high-resolution mission for GMES operational services: Remote Sensing of Environment, v. 120, p. 25–36, https://doi.org/10.1016/j.rse.2011.11.026.

Dwire, K.A., and Kauffman, J.B., 2003, Fire and riparian ecosystems in landscapes of the western USA: Forest Ecology and Management, v. 178, no. 1–2, p. 61–74, https://doi.org/10.1016/S0378-1127(03)00053-7.

Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., and Howard, S., 2007, A project for monitoring trends in burn severity: Fire Ecology, v. 3, no. 1, p. 3–21, https://doi.org/10.4996/fireecology.0301003.

ESRI, 2022, ArcGIS Pro (Version 2.8): ESRI, Inc., https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview (accessed 30 October 2023).

Fairfax, E., and Small, E.E., 2018, Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape: Ecohydrology, v. 11, no. 7, https://doi.org/10.1002/eco.1993.

Fairfax, E., and Whittle, A., 2020, Smokey the Beaver: Beaver-dammed riparian corridors stay green during wildfire throughout the western United States: Ecological Applications, v. 30, no. 8, https://doi.org/10.1002/eap.2225.

Feiner, K., and Lowry, C.S., 2015, Simulating the effects of a beaver dam on regional groundwater flow through a wetland: Journal of Hydrology–Regional Studies, v. 4, p. 675–685, https://doi.org/10.1016/j.ejrh.2015.10.001.

Finco, M., Quayle, B., Zhang, Y., Lecker, J., Megown, K.A., and Brewer, C.K., 2012, Monitoring trends and burn severity (MTBS): Monitoring wildfire activity for the past quarter century using Landsat data, *in* Morin, R.S., and Liknes, G.C., compilers, Proceedings: Moving from Status to Trends: Forest Inventory and Analysis (FIA) Symposium 2012, 4–6 December 2012, Baltimore, MD: U.S. Department of Agriculture Forest Service, Northern Research Station General Technical Report NRS-P-105, p. 222–228 [CD-ROM], https://www.fs.usda.gov/nrs/pubs/gtr/gtr_nrs-p-105.pdf.

Foster, C.N., Banks, S.C., Cary, G.J., Johnson, C.N., Lindenmayer, D.B., and Valentine, L.E., 2020, Animals as agents in fire regimes: Trends in Ecology & Evolution, v. 35, no. 4, p. 346–356, https://doi.org/10.1016/j.tree.2020.01.002.

Fouty, S.C., 2018, Euro-American beaver trapping and its long-term impact on drainage network form and function, water abundance, delivery, and system stability, *in* Johnson, R., Carothers, S.W., Finch, D.M., Kingsley, K.J., and Stanley, J.T., technical eds., Riparian Research and Management: Past, Present, Future: Volume 1: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-377, p. 102–133, https://doi.org/10.2737/RMRS-GTR-377.

Gable, T.D., Johnson-Bice, S.M., Homkes, A.T., Windels, S.K., and Bump, J.K., 2020, Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers: Science Advances, v. 6, no. 46, https://doi.org/10.1126/sciadv.abc5439.

Gilbert, J.T., Macfarlane, W.W., and Wheaton, J.M., 2016, The Valley Bottom Extraction Tool (V-BET): A GIS tool for delineating valley bottoms across entire drainage networks: Computers & Geosciences, v. 97, p. 1–14, https://doi.org/10.1016/j.cageo.2016.07.014.

Girden, E.R., 1992, ANOVA: Repeated Measures: Atlanta, Georgia, Sage Publications, Quantitative Applications in the Social Sciences 84, 88 p.

Google, 2022, Google Earth Pro (Version 7.3): Google, https://www.google.com/earth/versions/ (accessed October 2023).

Goss, M., Swain, D.L., Abatzoglou, J.T., Sarhadi, A., Kolden, C.A., Williams, A.P., and Diffenbaugh, N.S., 2020, Climate change is increasing the likelihood of extreme autumn wildfire conditions across California: Environmental Research Letters, v. 15, no. 9, 094016, https://doi.org/10.1088/1748-9326/ab83a7.

Gresswell, R.E., 1999, Fire and aquatic ecosystems in forested biomes of North America: Transactions of the American Fisheries Society, v. 128, no. 2, p. 193–221, https://doi.org/10.1577/1548-8659(1999)128<0193:FAAEIF>2.0.CO;2.

Gurnell, A., 1998, The hydrogeomorphological effects of beaver dam-building activity: Progress in Physical Geography, v. 22, no. 2, p. 167–189, https://doi.org/10.1177/030913339802200202.

Higuera, P.E., and Abatzoglou, J.T., 2021, Record-setting climate enabled the extraordinary 2020 fire season in the western United States: Global Change Biology, v. 27, no. 1, p. 1–2, https://doi.org/10.1111/gcb.15388.

Hillman, G.R., 1998, Flood wave attenuation by a wetland following a beaver dam failure on a second order boreal stream: Wetlands, v. 18, no. 1, p. 21–34, https://doi.org/10.1007/BF03161439.

Hood, G.A., and Bayley, S.E., 2008, Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada: Biological Conservation, v. 141, no. 2, p. 556–567, https://doi.org/10.1016/j.biocon.2007.12.003.

Hood, G.A., and Larson, D.G., 2015, Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands: Freshwater Biology, v. 60, no. 1, p. 198–208, https://doi.org/10.1111/fwb.12487.

Hyvönen, T., and Nummi, P., 2008, Habitat dynamics of beaver *Castor canadensis* at two spatial scales: Wildlife Biology, v. 14, no. 3, p. 302–308, https://doi.org/10.2981/0909-6396(2008)14[302:HDOBCC]2.0.CO;2.

Ives, R.L., 1942, The beaver-meadow complex: Journal of Geomorphology, v. 5, no. 3, p. 191–203.

Ji, L., Zhang, L., Wylie, B.K., and Rover, J., 2011, On the terminology of the spectral vegetation index (NIR − SWIR)/(NIR + SWIR): International Journal of Remote Sensing, v. 32, no. 21, p. 6901–6909, https://doi.org/10.1080/01431161.2010.510811.

Johnson, M.F., Thorne, C.R., Castro, J.M., Kondolf, G.M., Mazzacano, C.S., Rood, S.B., and Westbrook, C., 2019, Biomic river restoration: A new focus for river management: River Research and Applications, v. 36, no. 1, p. 3–12, https://doi.org/10.1002/rra.3529.

Johnston, C.A., 2017, Beavers: Boreal Ecosystem Engineers: Cham, Switzerland, Springer, 272 p., https://doi.org/10.1007/978-3-319-61533-2.

Jones, G., Kramer, H., Berigan, W., Whitmore, S., Gutiérrez, R., and Peery, M., 2021, Megafire causes persistent loss of an old-forest species: Animal Conservation, v. 24, no. 6, p. 925–936, https://doi.org/10.1111/acv.12697.

Jordan, C.E., and Fairfax, E., 2022, Beaver: The North American freshwater climate action plan: WIREs Water, v. 9 no. 4, https://doi.org/10.1002/wat2.1592.

Keeley, J.E., 2009, Fire intensity, fire severity and burn severity: A brief review and suggested usage: International Journal of Wildland Fire, v. 18, no. 1, p. 116–126, https://doi.org/10.1071/WF07049.

Khorshidi, M.S., Dennison, P.E., Nikoo, M.R., AghaKouchak, A., Luce, C.H., and Sadegh, M., 2020, Increasing concurrence of wildfire drivers tripled megafire critical danger days in Southern California between 1982 and 2018: Environmental Research Letters, v. 15, no. 10, 104002, https://doi.org/10.1088/1748-9326/abae9e.

Kirby, K., Buckley, G., and Mills, J., 2017, Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland: Folia Geobotanica, v. 52, no. 1, p. 5–13, https://doi.org/10.1007/s12224-016-9252-1.

Landesmann, J.B., and Morales, J.M., 2018, The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia: Plant Ecology, v. 219, no. 4, p. 455–466, https://doi.org/10.1007/s11258-018-0808-4.

Larsen, A., Larsen, J.R., and Lane, S.N., 2021, Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems: Earth-Science Reviews, v. 218, https://doi.org/10.1016/j.earscirev.2021.103623.

Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P., and Willby, N.J., 2017, Using ecosystem engineers as tools in habitat restoration and rewilding: Beaver and wetlands: The Science of the Total Environment, v. 605–606, p. 1021–1030, https://doi.org/10.1016/j.scitotenv.2017.06.173.

Le Breton, T.D., Lyons, M.B., Nolan, R.H., Penman, T., Williamson, G.J., and Ooi, M.K., 2022, Megafire-induced interval squeeze threatens vegetation at landscape scales: Frontiers in Ecology and the Environment, v. 20, p. 327–334, https://doi.org/10.1002/fee.2482.

Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege Bird, R., Duane, A., Fletcher, M.S., Giorgis, M.A., Haslem, A., Jones, G.M., Kelly, L.T., Lee, C.K.F., Nolan, R.H., Parr, C.L., Pausas, J.G., Price, J.N., Regos, A., Ritchie, E.G., Ruffault, J., Williamson, G.J., Wu, Q., and Nimmo, D.G., 2022, What do you mean, 'megafire'?: Global Ecology and Biogeography, v. 31, no. 10, p. 1906–1922, https://doi.org/10.1111/geb.13499.

Lowry, M.M., 1993, Groundwater Elevations and Temperature Adjacent to a Beaver Pond in Central Oregon [M.S. thesis]: Corvallis, Oregon, Oregon State University Department of Forest Engineering, 134 p.

MacCracken, J.G., Lebovitz, A.D., and Lewis, J.C., 2005, Selection of in-stream wood structures by beaver in the Bear River, southwest Washington: Northwestern Naturalist, v. 86, no. 2, p. 49–58, https://doi.org/10.1898/1051-1733(2005)086[0049:SOIWSB]2.0.CO;2.

Macfarlane, W.W., Wheaton, J.M., Bouwes, N., Jensen, M.L., Gilbert, J.T., Hough-Snee, N., and Shivik, J.A., 2015, Modeling the capacity of

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

riverscapes to support beaver dams: Geomorphology, v. 277, p. 72–99, https://doi.org/10.1016/j.geomorph.2015.11.019.

Magilligan, F.J., Nislow, K.H., Fisher, G.B., Wright, J., Mackey, G., and Laser, M., 2008, The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA: Geomorphology, v. 97, no. 3–4, p. 467–482, https://doi.org/10.1016/j.geomorph.2007.08.016.

Markle, C.E., Gage, H.J., Tekatch, A.M., Wilkinson, S.L., and Waddington, J.M., 2022, Wetland successional state affects fire severity in a boreal shield landscape: Wetlands, v. 42, no. 7, 87, https://doi.org/10.1007/s13157-022-01606-x.

Meddens, A.J., Kolden, C.A., Lutz, J.A., Smith, A.M., Cansler, C.A., Abatzoglou, J.T., Meigs, G.W., Downing, W.M., and Krawchuk, M.A., 2018, Fire refugia: What are they, and why do they matter for global change?: Bioscience, v. 68, no. 12, p. 944–954, https://doi.org/10.1093/biosci/biy103.

Miller, J.D., and Thode, A.E., 2007, Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR): Remote Sensing of Environment, v. 109, no. 1, p. 66–80, https://doi.org/10.1016/j.rse.2006.12.006.

Moran, P.A.P., 1950, Notes on continuous stochastic phenomena: Biometrika, v. 37, p. 17–23, https://doi.org/10.1093/biomet/37.1-2.17.

Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., and Beissinger, S.R., 2016, Managing climate change refugia for climate adaptation: PLoS One, v. 11, no. 8, https://doi.org/10.1371/journal.pone.0159909.

Naiman, R.J., Johnston, C.A., and Kelley, J.C., 1988, Alteration of North American streams by beaver: Bioscience, v. 38, no. 11, p. 753–762, https://doi.org/10.2307/1310784.

National Interagency Fire Center (NIFC), 2022, Wildland Fire Locations Full History: https://data-nifc.opendata.arcgis.com/ (accessed 30 October 2023).

Norman, L.M., Lal, R., Wohl, E., Fairfax, E., Gellis, A.C., and Pollock, M.M., 2022, Natural infrastructure in dryland streams (NIDS) can establish regenerative wetland sinks that reverse desertification and strengthen climate resilience: The Science of the Total Environment, v. 849, https://doi.org/10.1016/j.scitotenv.2022.157738.

Osei, N.A., Gurnell, A.M., and Harvey, G.L., 2015, The role of large wood in retaining fine sediment, organic matter and plant propagules in a small, single-thread forest river: Geomorphology, v. 235, p. 77–87, https://doi.org/10.1016/j.geomorph.2015.01.031.

Pedersen, E.J., Miller, D.L., Simpson, G.L., and Ross, N., 2019, Hierarchical generalized additive models in ecology: An introduction with mgcv: PeerJ, v. 7, https://doi.org/10.7717/peerj.6876.

Phillips, J.D., 2009, Biological energy in landscape evolution: American Journal of Science, v. 309, no. 4, p. 271–289, https://doi.org/10.2475/04.2009.01.

Phillips, J.D., 2016, Landforms as extended composite phenotypes: Earth Surface Processes and Landforms, v. 41, no. 1, p. 16–26, https://doi.org/10.1002/esp.3764.

Pleniou, M., and Koutsias, N., 2013, Sensitivity of spectral reflectance values to different burn and vegetation ratios: A multi-scale approach applied in a fire affected area: ISPRS Journal of Photogrammetry and Remote Sensing, v. 79, p. 199–210, https://doi.org/10.1016/j.isprsjprs.2013.02.016.

Pollock, M.M., Naiman, R.J., Erickson, H.E., Johnston, C.A., Pastor, J., and Pinay, G., 1995, Beaver as engineers—Influences on biotic and abiotic characteristics of drainage basins, *in* Jones, C.G., and Lawton, J.H., eds., Linking Species & Ecosystems: Boston, Springer, p. 117–126, https://doi.org/10.1007/978-1-4615-1773-3_12.

Pollock, M.M., Beechie, T.J., Wheaton, J.M., Jordan, C.E., Bouwes, N., Weber, N., and Volk, C., 2014, Using beaver dams to restore incised stream ecosystems: Bioscience, v. 64, no. 4, p. 279–290, https://doi.org/10.1093/biosci/biu036.

Pollock, M.M., Castro, J., Jordan, C.E., Lewallen, G., and Woodruff, K., 2015, The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains: Portland, Oregon, U.S. Fish and Wildlife Service, Version 1.02, 189 p., https://www.fws.gov/media/beaver-restoration-guidebook.

Polvi, L.E., and Wohl, E., 2012, The beaver meadow complex revisited—The role of beavers in post-glacial floodplain development: Earth Surface Processes and Landforms, v. 37, no. 3, p. 332–346, https://doi.org/10.1002/esp.2261.

Prein, A.F., Coen, J., and Jaye, A., 2022, The character and changing frequency of extreme California fire weather: Journal of Geophysical Research: Atmospheres, v. 127, e2021JD035350, https://doi.org/10.1029/2021JD035350.

Puttock, A., Graham, H.A., Ashe, J., Luscombe, D.J., and Brazier, R.E., 2021, Beaver dams attenuate flow: A multi-site study: Hydrological Processes, v. 35, no. 2, https://doi.org/10.1002/hyp.14017.

QGIS.org, 2022, QGIS Geographic Information System: QGIS Association, http://www.qgis.org (accessed 30 October 2023).

Rinne, J.N., 1996, Management briefs: Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States: North American Journal of Fisheries Management, v. 16, no. 3, p. 653–658, https://doi.org/10.1577/1548-8675(1996)016<0653:MBSTEO>2.3.CO;2.

Rodriguez, B., Lareau, N.P., Kingsmill, D.E., and Clements, C.B., 2020, Extreme pyroconvective updrafts during a megafire: Geophysical Research Letters, v. 47, no. 18, https://doi.org/10.1029/2020GL089001.

Ronnquist, A.L., and Westbrook, C.J., 2021, Beaver dams: How structure, flow state, and landscape setting regulate water storage and release: The Science of the Total Environment, v. 785, https://doi.org/10.1016/j.scitotenv.2021.147333.

Rood, S.B., and Mahoney, J.M., 1990, Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation: Environmental Management, v. 14, no. 4, p. 451–464, https://doi.org/10.1007/BF02394134.

Roy, D.P., Wulder, M.A., Loveland, T.R., Woodcock, C.E., Allen, R.G., Anderson, M.C., Helder, D., Irons, J.R., Johnson, D.M., Kennedy, R., Scambos, T.A., Schaaf, C.B., Schott, J.R., Sheng, Y., Vermote, E.F., Belward, A.S., Bindschadler, R., Cohen, W.B., Gao, F., Hipple, J.D., Hostert, P., Huntington, J., Justice, C.O., Kilic, A., Kovalskyy, V., Lee, Z.P., Lymburner, L., Masek, J.G., McCorkel, J., Shuai, Y., Trezza, R., Vogelmann, J., Wynne, R.H., and Zhu, Z., 2014, Landsat-8: Science and product vision for terrestrial global change research: Remote Sensing of Environment, v. 145, p. 154–172, https://doi.org/10.1016/j.rse.2014.02.001.

Roy, D.P., Huang, H., Boschetti, L., Giglio, L., Yan, L., Zhang, H.H., and Li, Z., 2019, Landsat-8 and Sentinel-2 burned area mapping—A combined sensor multi-temporal change detection approach: Remote Sensing of Environment, v. 231, https://doi.org/10.1016/j.rse.2019.111254.

Ruxton, G.D., and Beauchamp, G., 2008, Time for some a priori thinking about post hoc testing: Behavioral Ecology, v. 19, no. 3, p. 690–693, https://doi.org/10.1093/beheco/arn020.

Scamardo, J., and Wohl, E.E., 2019, Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado Front Range, USA: River Research and Applications, v. 36, p. 398–409, https://doi.org/10.1002/rra.3592.

Schier, G.A., Jones, J.R., and Winokur, R.P., 1985, Vegetative regeneration, *in* DeByle, N.V., and Winokur, R.P., eds., Aspen: Ecology and Management in the Western United States: U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-119, p. 29–33, https://doi.org/10.2737/RM-GTR-119.

Shinneman, D.J., Baker, W.L., Rogers, P.C., and Kulakowski, D., 2013, Fire regimes of quaking aspen in the Mountain West: Forest Ecology and Management, v. 299, p. 22–34, https://doi.org/10.1016/j.foreco.2012.11.032.

Short, L.E., Gabet, E.J., and Hoffman, D.F., 2015, The role of large woody debris in modulating the dispersal of a post-fire sediment pulse: Geomorphology, v. 246, p. 351–358, https://doi.org/10.1016/j.geomorph.2015.06.031.

Skidmore, P., and Wheaton, J., 2022, Riverscapes as natural infrastructure: Meeting challenges of climate adaptation and ecosystem restoration: Anthropocene, v. 38, https://doi.org/10.1016/j.ancene.2022.100334.

Skinner, C.N., and Chang, C., 1996, Fire regimes, past and present, *in* Sierra Nevada Ecosystem Project: Final Report to Congress. Volume II. Assessments and Scientific Basis for Management Options: Davis, California, Centers for Water and Wildland Resources, University of California, Wildland Resources Center Report 37, p. 1041–1069, https://pubs.usgs.gov/dds/dds-43/VOL_II/VII_C38.PDF.

Stein, S.J., Price, P.W., Abrahamson, W.G., and Sacchi, C.F., 1992, The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk: Oikos, v. 65, p. 190–196, https://doi.org/10.2307/3545009.

Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., and van Wagtendonk, J.W., 2014, Temperate and boreal forest mega-fires: Characteristics and challenges: Frontiers in Ecology and the Environment, v. 12, no. 2, p. 115–122, https://doi.org/10.1890/120332.

Swain, D.L., 2021, A shorter, sharper rainy season amplifies California wildfire risk: Geophysical Research Letters, v. 48, no. 5, https://doi.org/10.1029/2021GL092843.

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

Syphard, A.D., Radeloff, V.C., Keeley, J.E., Hawbaker, T.J., Clayton, M.K., Stewart, S.I., and Hammer, R.B., 2007, Human influence on California fire regimes: Ecological Applications, v. 17, no. 5, p. 1388–1402, https://doi.org/10.1890/06-1128.1.

Thompson, D.M., and Stull, G.N., 2002, The development and historic use of habitat structures in channel restoration in the United States: The grand experiment in fisheries management: Géographie Physique et Quaternaire, v. 56, no. 1, p. 45–60, https://doi.org/10.7202/008604ar.

U.S. Geological Survey (USGS), 2019 National Hydrography Dataset, Version USGS National Hydrography Dataset Best Resolution (NHD): https://www.usgs.gov/national-hydrography/access-national-hydrography-products (accessed 30 October 2023).

van Mantgem, P.J., and Schwilk, D.W., 2009, Negligible influence of spatial autocorrelation in the assessment of fire effects in a mixed conifer forest: Fire Ecology, v. 5, no. 2, p. 116–125, https://doi.org/10.4996/fireecology.0502116.

Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I., 2010, A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index: Journal of Climate, v. 23, no. 7, p. 1696–1718, https://doi.org/10.1175/2009JCLI2909.1.

Weirich, J., 2020, Beaver Moderated Fire Resistance in the North Cascades [M.S. thesis]: Cheney, Washington, Eastern Washington University, 56 p.

Welch, B., 1947, The generalization of 'student's' problem when several different population variances are involved: Biometrika, v. 34, no. 1–2, p. 28–35, https://doi.org/10.2307/2332510.

Westbrook, C.J., Cooper, D.J., and Baker, B.W., 2006, Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area: Water Resources Research, v. 42, no. 6, W06404, https://doi.org/10.1029/2005WR004560.

Westbrook, C.J., Ronnquist, A., and Bedard-Haughn, A., 2020, Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm: Hydrological Processes, v. 34, no. 18, p. 3726–3737, https://doi.org/10.1002/hyp.13828.

Wheaton, J., Bennett, S.N., Bouwes, N., Maestas, J.D., and Shahverdian, S.M., 2019, Low-Tech Process-Based Restoration of Riverscapes: Design Manual: Logan, Utah, Utah State University Restoration Consortium, 286 p.

Whipple, A., 2019, Riparian Resilience in the Face of Interacting Disturbances: Understanding Complex Interactions between Wildfire, Erosion, and Beaver (*Castor canadensis*) in Grazed Dryland Riparian Systems of Low Order Streams in North Central Washington State, USA [M.S. thesis]: Cheney, Washington, Eastern Washington University, 114 p.

Williams, J., 2013, Exploring the onset of high-impact mega-fires through a forest land management prism: Forest Ecology and Management, v. 294, p. 4–10, https://doi.org/10.1016/j.foreco.2012.06.030.

Wohl, E., 2011, What should these rivers look like? Historical range of variability and human impacts in the Colorado Front Range, USA: Earth Surface Processes and Landforms, v. 36, no. 10, p. 1378–1390, https://doi.org/10.1002/esp.2180.

Wohl, E., 2015, Of wood and rivers: Bridging the perception gap: WIREs Water, v. 2, no. 3, p. 167–176, https://doi.org/10.1002/wat2.1076.

Wohl, E., 2021a, An integrative conceptualization of floodplain storage: Reviews of Geophysics, v. 59, no. 2, https://doi.org/10.1029/2020RG000724.

Wohl, E., 2021b, Legacy effects of loss of beavers in the continental United States: Environmental Research Letters, v. 16, no. 2, p. 025010, https://doi.org/10.1088/1748-9326/abd34e.

Wohl, E., and Scott, D.N., 2016, Wood and sediment storage and dynamics in river corridors: Earth Surface Processes and Landforms, v. 42, no. 1, p. 5–23, https://doi.org/10.1002/esp.3909.

Wohl, E., Lane, S.N., and Wilcox, A.C., 2015, The science and practice of river restoration: Water Resources Research, v. 51, no. 8, p. 5974–5997, https://doi.org/10.1002/2014WR016874.

Wohl, E., Castro, J., Cluer, B., Merritts, D., Powers, P., Staab, B., and Thorne, C., 2021, Rediscovering, reevaluating, and restoring lost river-wetland corridors: Frontiers in Earth Science, v. 9, https://doi.org/10.3389/feart.2021.653623.

Wohl, E., Marshall, A.E., Scamardo, J., White, D., and Morrison, R.R., 2022, Biogeomorphic influences on river corridor resilience to wildfire disturbances in a mountain stream of the Southern Rockies, USA: The Science of the Total Environment, v. 820, https://doi.org/10.1016/j.scitotenv.2022.153321.

Woo, M.-K., and Waddington, J.M., 1990, Effects of beaver dams on subarctic wetland hydrology: Arctic, v. 43, no. 3, p. 223–230, https://doi.org/10.14430/arctic1615.

Wood, S.N., 2018, Mixed GAM Computation Vehicle with Automatic Smoothness Estimation: CRAN, https://cran.uib.no/web/packages/mgcv/mgcv.pdf (accessed 30 October 2023).

Manuscript Accepted by the Society 8 November 2023
Manuscript Published Online 15 January 2024

Printed in the USA

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

Downloaded from http://pubs.geoscienceworld.org/books/book/chapter-pdf/6193389/spe562-07.pdf
by Boulder Labs Library Periodicals - MC5 user

Check for updates

Communications

Ecological Applications, 30(8), 2020, e02225
© 2020 by the Ecological Society of America

Smokey the Beaver: beaver-dammed riparian corridors stay green during wildfire throughout the western United States

Emily Fairfax [1,3] and Andrew Whittle[2]

[1]*Department of Environmental Science and Resource Management, California State University Channel Islands, Camarillo, California 93012 USA*
[2]*Department of Geology and Geological Engineering, Colorado School of Mines, Golden, Colorado 80401 USA*

Citation: Fairfax, E., and A. Whittle. 2020. Smokey the Beaver: beaver-dammed riparian corridors stay green during wildfire throughout the western USA. Ecological Applications 30(8):e02225. 10.1002/eap.2225

Abstract. Beaver dams are gaining popularity as a low-tech, low-cost strategy to build climate resiliency at the landscape scale. They slow and store water that can be accessed by riparian vegetation during dry periods, effectively protecting riparian ecosystems from droughts. Whether or not this protection extends to wildfire has been discussed anecdotally but has not been examined in a scientific context. We used remotely sensed Normalized Difference Vegetation Index (NDVI) data to compare riparian vegetation greenness in areas with and without beaver damming during wildfire. We include data from five large wildfires of varying burn severity and dominant landcover settings in the western United States in our analysis. We found that beaver-dammed riparian corridors are relatively unaffected by wildfire when compared to similar riparian corridors without beaver damming. On average, the decrease in NDVI during fire in areas without beaver is 3.05 times as large as it is in areas with beaver. However, plant greenness rebounded in the year after wildfire regardless of beaver activity. Thus, we conclude that, while beaver activity does not necessarily play a role in riparian vegetation post-fire resilience, it does play a significant role in riparian vegetation fire resistance and refugia creation.

Key words: *beaver; burn; dam; drought; Normalized Difference Vegetation Index; remote sensing; riparian; vegetation; wildfire.*

Introduction

Beavers are native to North America (*Castor canadensis*) and to Eurasia (*Castor fiber*; Naiman et al. 1988, Wróbel 2020). They occupy a variety of landscapes, including mountain streams, lowland valleys, coastal estuaries, deserts, arctic tundra, and temperate forests. (Naiman et al. 1988, Leidholt-Bruner et al. 1992, Pilliod et al. 2017, Tape et al. 2018). Beavers are well known ecosystems engineers; they build channel-spanning dams from wood, stone, and mud that ultimately create the broad ponds and wetlands that beavers thrive in (Hammerson 1994). Beavers also excavate mud from the pond bottom and dig channels (also referred to as canals) radiating from the pond out into the surrounding landscape, which fill with water and increase their area of influence (Gurnell 1998). The combination of building flow obstructions (dams), accumulating water (ponds), and spreading that water out in the landscape (channels) gives beavers the unique potential to modulate environmental extremes such as flood and drought (Hood and Bayley 2008, Pilliod et al. 2017, Fairfax and Small 2018, Westbrook et al. 2020). When it comes to water, beavers slow it, spread it, and store it.

Due to the fact that beaver channels and dams spread water out in the landscape and store it broadly in adjacent soils (Fig. 1, top), the vegetation near beaver ponds doesn't experience as much reduced water availability during drought (Macfarlane et al. 2016, Pilliod et al. 2017, Fairfax and Small 2018; Fig. 1, middle). Drought-stricken vegetation burns more easily than lush, green vegetation (Liu et al. 2010), so it follows that the vegetation around beaver ponds would be more difficult to burn than vegetation around undammed creeks (Fig. 1, bottom). Although this concept has been observed, discussed, and documented in photographs (Fig. 2), the

Manuscript received 6 May 2020; revised 29 June 2020; accepted 24 August 2020. Corresponding Editor: Nancy F. Glenn.
[3] E-mail: emily.fairfax@csuci.edu

Communications

potential difference in vegetation health during wildfire in areas with and without beaver has not yet been quantified (Foster et al. 2020). In this study, we use satellite-derived Normalized Difference Vegetation Index (NDVI) data from the year before, year of, and year after a major wildfire to examine the vegetation changes of riparian corridors with and without beaver. We include data from five large wildfires located in five different western U.S. states, Colorado, California, Oregon, Idaho, and Wyoming, to quantify the extent to which, if any, vegetation in beaver-dammed riparian areas can stay green during wildfire.

Methods

Site selections and descriptions

We examined fires with differing burn severities and landcover to help determine whether the response of riparian areas with beaver-dam complexes to wildfire could be generalized beyond specific case studies. Table 1 provides a brief summary of the fires included in this study and the data used for each. The fires included in this study occurred in a variety of landcover types as determined by the 2016 National Landcover Database (Homer et al. 2020). Three of the fires studied occurred in shrubland dominant landscapes, and two occurred in forest dominant landscapes. The burn severity of the fires varied as well, with three fires that were majority unburned to low burn severity, and two fires that were majority moderate to high burn severity. Burn severity and fire perimeters were collected from the Monitoring Trends in Burn Severity Database and the GeoMAC Wildland Fire Support Database. (Eidenshink et al. 2007, USGS 2019). Fires occurred in areas with varying drought status in the years before, of, and after the fire. Drought severity was determined using the Palmer Drought Severity Index from the NOAA Gridded Climate Divisional Dataset (Palmer 1965, Vose et al. 2014). Full detailed fire information can be found in Appendix S1: Table S1.

Each fire contained creeks with heterogeneous patches of beaver activity. We determined where beavers were influencing riparian corridors in our study by locating and recording the position of beaver dams, ponds, and beaver-dug channels using satellite images acquired through Google Earth. Previous studies have successfully used aerial imagery and Google Earth to locate and identify beaver dams (Macfarlane et al. 2015, Puttock et al. 2015, Fairfax and Small 2018).

General process for evaluating impact of beavers on riparian wildfire resistance

Our procedure to determine whether, and to what extent, beaver activity protects riparian vegetation during wildfire is outlined below and again graphically in Appendix S2: Fig. S1.

(1). Collect geospatial (e.g., coordinates of dams, pond area polygon, dam length vectors) for each beaver dam within the fire perimeters.
(2). Extract remotely sensed NDVI along each creek that had patches of beaver activity on approximate date (month and day) of wildfire in year before, during, and after wildfire.

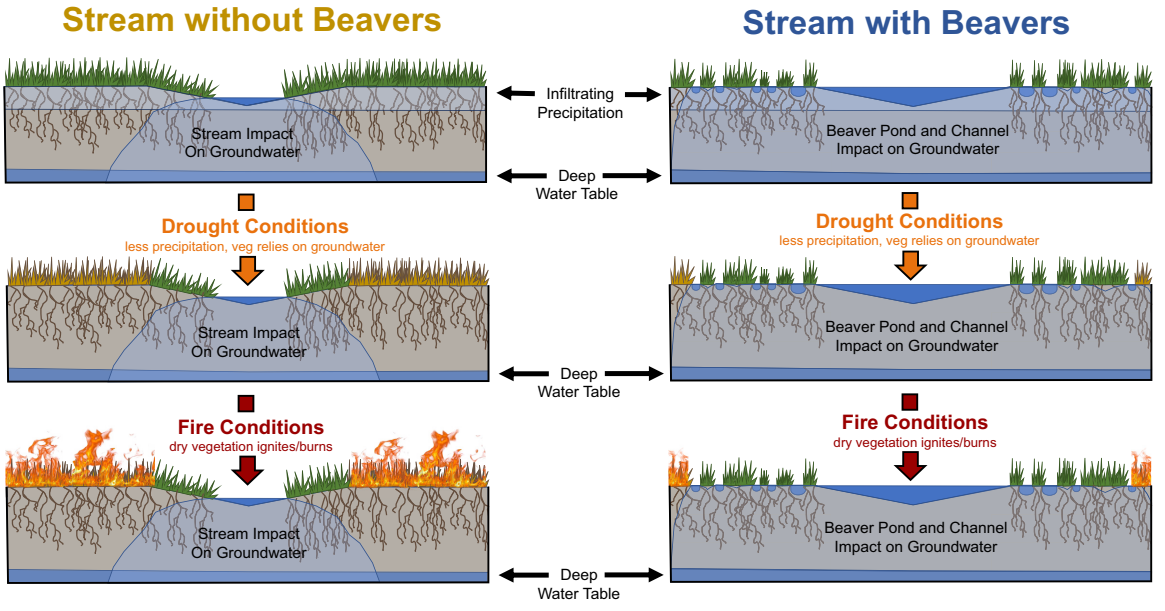


Fig. 1. Conceptual model of vegetation response to normal conditions (top), drought (middle), and fire (bottom) in creeks with (right) and without (left) beaver. [Color figure can be viewed at wileyonlinelibrary.com]

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



FIG. 2. Photographs of vegetation response to wildfire around beaver ponds. In both examples, vegetation near beaver ponds stayed green while other nearby riparian vegetation burned. (A) Adjacent creeks with and without beaver damming during the Manter Fire in California. Photograph from the Burned Area Emergency Response (BAER) team. (B) A creek with a beaver pond on it in Oregon prior to the Buzzard Complex Fire. (C) The same location as B, except image is from immediately after the wildfire (Google Earth). 1 foot = 0.30 m. [Color figure can be viewed at wileyonlinelibrary.com]

(3). Difference between pre-fire NDVI and fire NDVI is calculated at each site and graphically compared to locations of beaver dams.

(4). Divide creeks into sections broadly impacted by beaver activity and sections that do not have beaver activity, unscaled NDVI Differences in beaver and non-beaver areas are compared at the creek and wildfire scales.

(5). Use the maximum NDVI Difference on each creek to scale the changes in NDVI so sites can be compared while accounting for variation in burn severity, landcover, and climate.

(6). Compare scaled NDVI changes in areas with and without beaver across all study sites.

Following these steps allows us to move from site-specific case studies of individual creeks within larger wildfire-impacted landscapes, to generalized vegetation response to wildfire in riparian corridors with and without beaver activity.

NDVI collection and calculations

Previous studies indicate that Normalized Difference Vegetation Index (NDVI) can be used as a proxy for overall riparian vegetation health, and that it can be estimated from remotely sensed data (Macfarlane et al. 2016). High NDVI (values close to 1) generally indicated lusher, greener vegetation while very low NDVI (values close to 0 or negative) generally indicate unhealthy, senesced, or dying vegetation. In more densely vegetated areas, including riparian zones, an NDVI below 0.3 is considered to be indicative of low plant health and productivity (Nagler et al. 2001, Donnelly et al. 2016, Huntington et al. 2016, Silverman et al. 2019). In this study, we use the 0.3 NDVI threshold, Google Earth aerial imagery, and landcover data to determine where riparian vegetation is present before the fires.

Apart from the 2000 Manter Fire in California, we calculated NDVI from Landsat 8 imagery. Landsat 8 imagery is available from April 2013 through the present, has 30 × 30 m pixel resolution on its red (R) and near-infrared (NIR) bands, and a 16-d recurrence interval. For the Manter Fire, we used Landsat 7 imagery. Landsat 7 imagery is available from April 1999 through the present and has the same pixel resolution in R and NIR and recurrence interval as Landsat 8. The Landsat imagery dates used for each fire are summarized in Appendix S1: Table S1 and were chosen based on timing and cloud-free status. The NDVI is calculated from Landsat acquired reflectivity data according to Eq. 1 (Tucker 1979):

$$\mathrm{NDVI} = (\mathrm{NIR}x02010; \mathrm{RED})/(\mathrm{NIR} + \mathrm{RED}) \quad (1)$$

where NIR is the near-infrared band reflectivity and RED is the red band reflectivity. All images came with a

TABLE 1. Brief summary of fire information included in study.

State	Year	Name	Area within perimeter (acres)	No. beaver dams	Burn severity (%; unburned–low/moderate/high)	Dominant landcover
California	2000	Manter	79,182	57	46/32/22	shrubland
Colorado	2016	Beaver Creek	38,380	364	38/23/39	forest
Idaho	2018	Sharps	64,811	62	57/43/<1	shrubland
Oregon	2014	Buzzard Complex	395,348	48	87/13/<1	shrubland
Wyoming	2018	Badger Creek	21,322	190	54/36/10	forest

Note: 1 acre = 0.40 ha.

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

quality assessment statement regarding whether the integrity of data had been affected by instrument artifacts or atmospheric conditions and were sourced directly from the USGS Earth Resources Observation and Science (EROS) Center Science Processing Architecture (ESPA; USGS 2014). We extracted NDVI values at each pixel immediately adjacent to the creek (≤30 m distance from creek edge) for all creeks in the study in the year before, the year of, and the year after the fire on the approximate date (month and day) of the wildfire. Higher values indicate greener vegetation. This narrow area is the most heavily and consistently impacted by beaver activity and least likely to be influenced by short term changes in beaver occupancy. However, beaver activity often supports riparian vegetation well beyond the 30 m radius (Gurnell 1998). A larger data set with on-ground riparian zone surveys before, during, and after wildfire would be needed to robustly quantify the total area of riparian zone influenced by beaver activity. In the absence of that data, our results should be interpreted as a conservative assessment of the refugia that beavers can support during wildfires.

Vegetation response to wildfire was calculated by subtracting the NDVI during the wildfire from the NDVI at the same time of year in the year prior to the wildfire

$$\text{NDVI Difference} = \text{NDVI}_{\text{prex02010;fire}}x02010; \text{NDVI}_{\text{fire}}. \quad (2)$$

With this formulation, smaller values for NDVI difference indicate greater resistance to wildfire, i.e., the plants stayed greener and burned less. This type of formulation has been utilized in prior work to evaluate change in vegetation condition as a response to environmental stressors (Nagler et al. 2001, Macfarlane et al. 2016, Fairfax and Small 2018, Silverman et al. 2019).

We considered the 95th percentile NDVI difference value to be the maximum NDVI difference occurring on each creek. These values are the scaling factors that allow for comparisons between creeks and wildfires while accounting for burn heterogeneity within fire perimeters and variations in vegetation cover, climate, and burn intensity between fires using the following formulation:

$$\text{Scaled NDVI difference} = (\text{NDVI difference})/(\text{Max NDVI difference on creek}). \quad (3)$$

The lower the scaled NDVI difference value, the more fire resistant the riparian vegetation in that section of creek is. We used the scaled NDVI difference calculated for each pixel along each creek to generate two populations of data: one from sections of creek that had beaver activity, one from sections of creek that did not have beaver activity. To be considered part of a section with beaver damming, it had to be within 30 m longitudinally of a beaver pond, dam, or channel. This is a conservative estimate of the spatial scale of hydrologic connectivity around beaver ponds (Wegener et al. 2017). Each population of data contains data from multiple creeks, fires, landcover types, burn intensities, climate histories, and years, thus the results of comparing the populations should be considered more generalizable than only comparing within a given creek or wildfire perimeter. In addition to comparing mean values and general distributions of data, we perform statistical comparisons to quantify the significance of our results. We use the Kolmogorov-Smirnov (KS) test (Massey 1951) and the Welch two-sample *t* test (Welch 1947). The KS test evaluates whether two populations of data come from a single distribution of data or two distinct distributions, and the *t* test evaluates the likelihood that both samples have identical mean values. For all tests, $P < 0.05$ was our threshold for significance. The population size of pixels used for statistical tests of NDVI difference at the creek scale, wildfire scale, and combined data scale are in Appendix S4: Tables S1 and S2.

Results

NDVI along creek profiles

We collected the NDVI along each creek in the study in the year before, during, and after the fire on the approximate date (month and day) of the wildfire. Our data from a creek in the Manter Fire in California is shown in Fig. 3 and is representative of the results we saw across all creeks. In Fig. 3 (top), the locations of beaver dams are marked along the *x*-axis with black squares. Higher NDVI values indicate greener vegetation. The full set of plots showing NDVI before, during, and after fire as a function of distance along creek can be found in Appendix S3: Fig. S1.

From the pre/during NDVI profiles along each creek, we calculated the NDVI difference (Eq. 2) and again plotted it as a function of distance along creek with the position of beaver dams marked by black boxes. Fig. 3 (bottom) shows the NDVI difference plot derived from the data in Fig. 3 (top). The full set of plots showing NDVI difference as a function of distance along creek can be found in Appendix S4: Fig. S1. A lower NDVI difference value indicates greater resistance to wildfire, i.e., plants in that area are burning less if at all. These NDVI difference profiles were split into sections with and without beaver damming according to the criteria listed in *Methods: NDVI collection and calculations.* From the 12 creeks in the study, we ultimately split them into a total of 61 sections: 32 sections with beaver damming and 29 sections without beaver damming. We calculated the maximum NDVI Difference value for each creek, which is used as the scaling factor to allow comparisons between creeks. These are summarized in Appendix S4: Table S1.

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

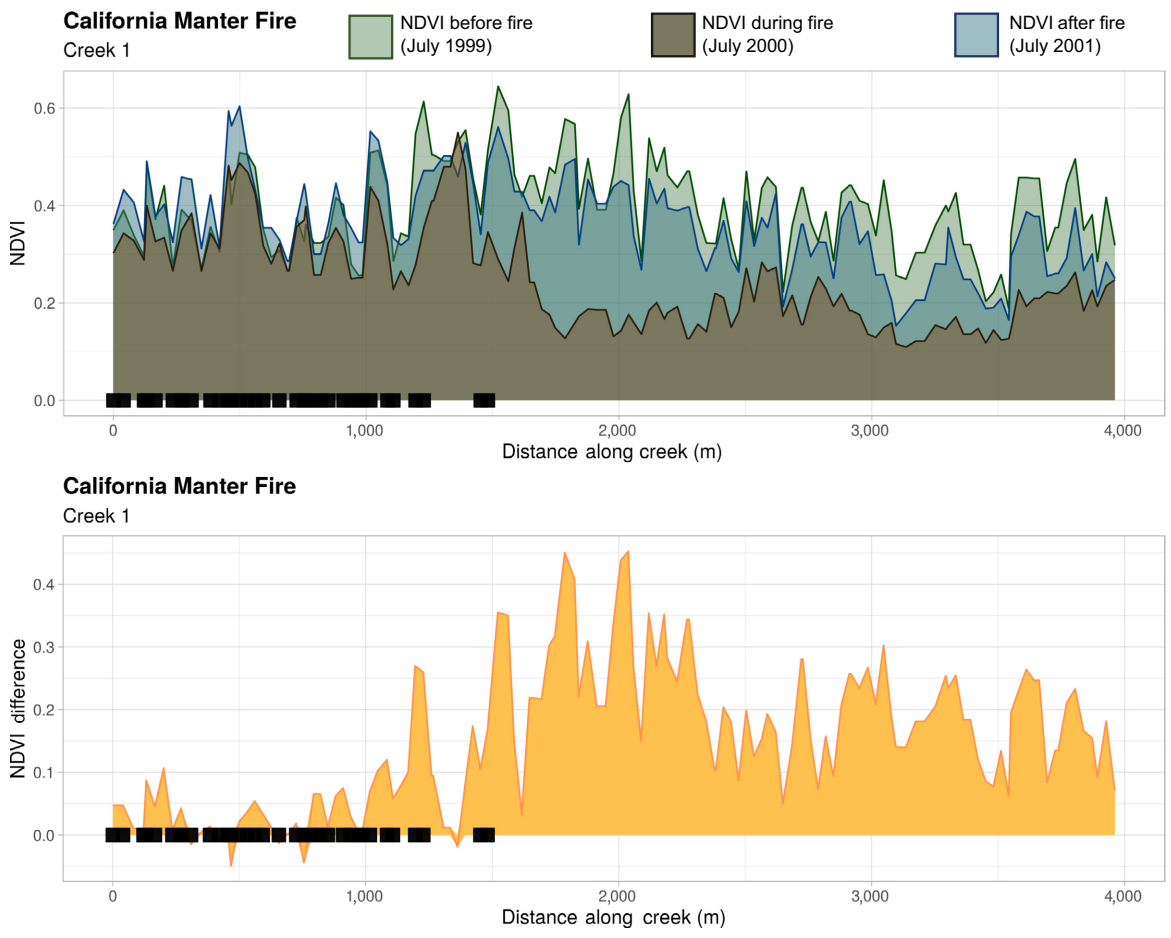


FIG. 3. (Top) NDVI before (green), during (brown), and after (blue) wildfire along a creek in California during the 2000 Manter Fire. Higher NDVI values indicate greener plants. (Bottom) NDVI Difference (Pre-Fire NDVI minus Fire NDVI) along the same creek. The locations of beaver dams are marked with black squares along the *x*-axis. [Color figure can be viewed at wileyonlinelibrary.com]

Unscaled and scaled NDVI differences from all sites

We determined that beaver impacted areas had significantly higher NDVI on the individual creek scale (unscaled NDVI difference), within a wildfire (unscaled NDVI difference), and in our combined data (scaled NDVI difference). The full set of box and whisker plots detailing these results are in Fig. 4. The average scaled NDVI difference in sections of creek without beaver activity was 3.05 times larger than in areas with beaver activity (0.58 without beavers, 0.19 with beavers). These differences were significant using both statistical tests, with $P < 0.001$. We compared pre-fire to post-fire NDVI in areas with beaver vs areas without beaver to probe whether beaver damming may also play a role in riparian corridor recovery in the year after a fire occurs. The full details of these comparisons can be found in Appendix S4: Table S3. We found very little difference (average NDVI difference = 0.07) between pre-fire and post-fire NDVI, and that beaver activity was not correlated with whether the pre-fire or post-fire year was greener (higher NDVI). Thus, the ability for a burned riparian area to rebound after fire is not dependent on beaver activity.

DISCUSSION

Our results indicate that beaver damming plays a significant role in protecting riparian vegetation during wildfires, and that this is a consistently observable phenomenon across landscapes. The riparian vegetation near beaver dams maintained NDVI values during wildfire that were similar to their pre-fire values. Meanwhile the riparian NDVI was significantly reduced from its pre-fire value when not near a beaver dam. The scaled NDVI differences in sections of creek that did not have beaver were on average more than three times as affected by fire as areas that had beaver. This is consistent with our conceptual model for fire resistance (Fig. 1) and with observed fire burn patterns around beaver ponds (Fig. 2). When a fire does ignite, our data suggests that the beaver-dammed riparian areas have stored water that

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Communications

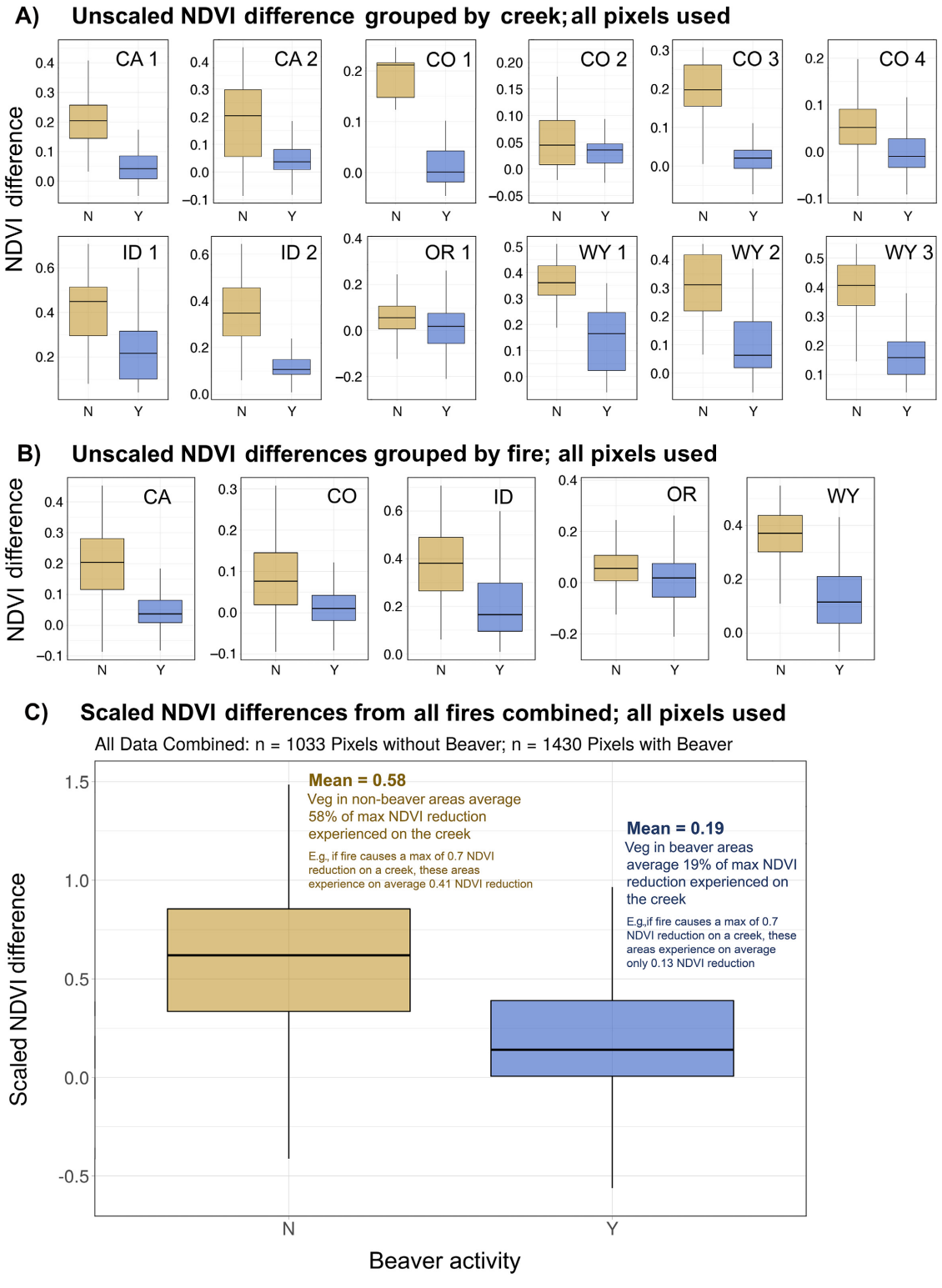


FIG. 4. Box plots of NDVI difference (pre-fire NDVI minus fire NDVI) in beaver (Y) vs. non-beaver (N) areas at three scales: (A) individual creek scale, (B) wildfire scale, and (C) all data combined. Lower absolute NDVI difference and scaled NDVI difference values indicate greater vegetation (veg) resistance to wildfire, i.e., plants burned less. The difference in means and distributions for every box plot shown was statistically significant ($P < 0.05$). NDVI Differences are unscaled in panels A and B. NDVI differences are scaled by the maximum (max) NDVI difference in panel C. [Color figure can be viewed at wileyonlinelibrary.com]

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

kept plants hydrated enough to make it energetically unfavorable to burn. It's similar to trying to start a fire with a pile of wet leaves versus with dry kindling.

These ribbons of fire-resistant riparian corridor may be particularly important for species that are unable to physically escape wildfire. They can provide temporary habitat for fish, amphibians, reptiles, small mammals, wild and domestic ungulates, and birds that are unable to outrun/outfly the spread of flames. While we found that beaver activity does play a significant role in maintaining vegetation greenness during wildfires, it does not appear to play a significant role in the ability for a riparian corridor to rebound in the year following fire. Riparian vegetation NDVI rebounded in the year following the fire regardless of proximity to beaver activity. Thus, we would describe beaver activity as creating refugia during wildfire, but not necessarily changing the long-term landscape outcomes.

The western United States used to have much more wetland area than it does today, so it is possible that historically beavers were less necessary for creating fire-resistant landscape patches (Mitsch and Gosselink 1993). But as it stands today, wetland habitat is very limited and beavers can create and maintain wetland habitat that persists through flood, drought, and, as we have shown in this study, fire. This has immediate relevance to scientists and practitioners across the North America and Eurasia, particularly in places with increasing wildfire risk and existing or planned beaver populations. Perhaps instead of relying solely on human engineering and management to create and maintain fire-resistant landscape patches, we could benefit from beaver's ecosystem engineering to achieve the same goals at a lower cost.

Acknowledgments

This research was conducted with Government support under and awarded by Department of Defense, Air Force Office of Scientific Research, National Defense Science and Engineering Graduate (NDSEG) Fellowship, 32 CFR 168a. Emily Fairfax also received support from the Birkeland Graduate Scholarship and the Penny Patterson Graduate Scholarship. Andrew Whittle received support from the University of Colorado Boulder Department of Geological Sciences. We thank Suzanne Fouty for her support during the initial drafting of this manuscript. We thank the editors and reviewers for their thoughtful suggestions and feedback. Author contributions: Andrew Whittle, methodology (equal); Emily Fairfax, methodology (equal), conceptualization (lead), formal analysis (lead), writing (lead). The authors do not have any conflicts of interest.

Literature Cited

Donnelly, J., D. E. Naugle, C. A. Hagen, and J. D. Maestas. 2016. Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions. Ecosphere 7:e01208.

Eidenshink, J., B. Schwind, K. Brewer, Z.-L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire ecology 3:3–21.

Fairfax, E., and E. E. Small. 2018. Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape. Ecohydrology 11:e1993.

Foster, C. N., S. C. Banks, G. J. Cary, C. N. Johnson, D. B. Lindenmayer, and L. E. Valentine. 2020. Animals as agents in fire regimes. Trends in Ecology & Evolution 35:346–356.

Gurnell, A. 1998. The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22:167–189.

Hammerson, G. A. 1994. Beaver (*Castor canadensis*): Ecosystem alterations, management, and monitoring. Natural Areas Journal 14:44–57.

Homer, C. et al 2020. Conterminous United States land cover change patterns 2001–2016 from the 2016 National Land Cover Database. ISPRS Journal of Photogrammetry and Remote Sensing 162:184–199.

Hood, G. A., and S. E. Bayley. 2008. Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biological Conservation 141:556–567.

Huntington, J., K. McGwire, C. Morton, K. Snyder, S. Peterson, T. Erickson, R. Niswonger, R. Carroll, G. Smith, and R. Allen. 2016. Assessing the role of climate and resource management on groundwater dependent ecosystem changes in arid environments within the Landsat archive. Remote Sensing of Environment 185:186–197.

Leidholt-Bruner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundacne of coho salmon fry in two coastal oregon streams. Northwest Science 66:218–223.

Liu, Y., J. Stanturf, and S. Goodrick. 2010. Trends in global wildfire potential in a changing climate. Forest Ecology and Management 259:685–697.

Macfarlane, W. W., J. T. Gilbert, M. L. Jensen, J. D. Gilbert, N. Hough-Snee, P. A. McHugh, J. M. Wheaton, and S. N. Bennett. 2016. Riparian vegetation as an indicator of riparian condition: Detecting departures from historic condition across the North American West. Journal of Environmental Management 202:447–460.

Macfarlane, W. W., J. M. Wheaton, N. Bouwes, M. L. Jensen, J. T. Gilbert, N. Hough-Snee, and J. A. Shivik. 2015. Modeling the capacity of riverscapes to support beaver dams. Geomorphology 277:72–99.

Massey, F. J. 1951. The Kolmogorov-Smirnov test for goodness of fit. Journal of the American Statistical Association 46:68–78.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Second edition. John Wiley, New York, New York, USA.

Nagler, P. L., E. P. Glenn, and A. R. Huete. 2001. Assessment of spectral vegetation indices for riparian vegetation in the Colorado River delta, Mexico. Journal of Arid Environments 49:91–110.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.

Palmer, W. C.1965. Meteorological drought. Research Paper 45. U.S. Department of Commerce, Washington, D.C., USA.

Pilliod, D. S., A. T. Rohde, S. Charnley, R. R. Davee, J. B. Dunham, H. Gosnell, G. E. Grant, M. B. Hausner, J. L. Huntington, and C. Nash. 2017. Survey of beaver-related restoration practices in rangeland streams of the western USA. Environmental Management 61:58–68.

Puttock, A., A. Cunliffe, K. Anderson, and R. E. Brazier. 2015. Aerial photography collected with a multirotor drone reveals impact of Eurasian beaver reintroduction on ecosystem structure. Journal of Unmanned Vehicle Systems 3:123–130.

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Silverman, N. L., B. W. Allred, J. P. Donnelly, T. B. Chapman, J. D. Maestas, J. M. Wheaton, J. White, and D. E. Naugle. 2019. Low-tech riparian and wet meadow restoration increases vegetation productivity and resilience across semiarid rangelands. Restoration Ecology 27:269–278.

Tape, K. D., B. M. Jones, C. D. Arp, I. Nitze, and G. Grosse 2018. Tundra be dammed: Beaver colonization of the Arctic. Global Change Biology 24:4478–4488.

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment 8:127–150.

USGS. 2014. Earth resources observation and science (EROS) center science processing architecture (ESPA) on demand interface. USGS, Sioux Falls, South Dakota, USA.

USGS. 2019. GeoMAC Wildland Fire Database. USGS, Reston, Virginia, USA.

Vose, R. S., S. Applequist, M. Squires, I. Durre, M. J. Menne, C. N. Williams, C. Fenimore, K. Gleason, and D. Arndt.2014. NOAA's Gridded Climate Divisional Dataset (CLIMDIV). https://doi.org/10.7289/V5M32STR

Wegener, P., T. Covino, and E. E. Wohl. 2017. Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. Water Resources Research 53:4606–4623.

Welch, B. 1947. The generalization of 'Student's' problem when several different population variances are involved. Biometrika 34:28–35.

Westbrook, C. J., A. Ronnquist, and A. Bedard-Haughn. 2020. Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm. Hydrological Processes. https://doi.org/10.1002/hyp.13828.

Wróbel, M.. 2020. Population of Eurasian beaver (Castor fiber) in Europe. Global Ecology and Conservation 23:e01046.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2225/full

Data Availability Statement

The data that support the findings of this study are openly available in Pangaea at https://doi.pangaea.de/10.1594/PANGAEA.900944.

19395582, 2020, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2225, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

PLOS ONE

RESEARCH ARTICLE

Livestock management, beaver, and climate influences on riparian vegetation in a semi-arid landscape

Kurt A. Fesenmyer[1]*, Daniel C. Dauwalter[1], Carol Evans[2¤], Todd Allai[3]

1 Trout Unlimited, Boise, Idaho, United States of America, **2** US Bureau of Land Management, Elko, Nevada, United States of America, **3** US Bureau of Land Management, Vale, Oregon, United States of America

¤ Current address: Retired, Spring Creek, Nevada, United States of America
* kfesenmyer@tu.org

Check for updates

OPEN ACCESS

Citation: Fesenmyer KA, Dauwalter DC, Evans C, Allai T (2018) Livestock management, beaver, and climate influences on riparian vegetation in a semi-arid landscape. PLoS ONE 13(12): e0208928. https://doi.org/10.1371/journal.pone.0208928

Editor: Emmanuel Serrano Ferron, Universitat Autonoma de Barcelona, SPAIN

Received: July 10, 2018

Accepted: November 26, 2018

Published: December 11, 2018

Copyright: This is an open access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful purpose. The work is made available under the Creative Commons CC0 public domain dedication.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was funded by the Bureau of Land Management under cooperative agreement L14AC00009 with Trout Unlimited. Bureau of Land Management staff had a role in conceptualizing the analysis and preparing the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abstract

Riparian and aquatic habitats support biodiversity and key environmental processes in semi-arid and arid landscapes, but stressors such as conventional livestock grazing, wildfire, and drought can degrade their condition. To enhance habitat for fish and wildlife and increase resiliency in these critical areas, land managers in the interior western United States increasingly use alternative grazing strategies, beaver management, or beaver dam surrogates as low-effort, low-expense restoration approaches. In this study we used historical archives of satellite and aerial imagery spanning three decades to characterize riparian vegetation productivity and document beaver dam occurrences, then evaluated vegetation productivity relative to land management associated with livestock grazing and beaver dam densities while accounting for climate and wildfire. After controlling for stream characteristics such as stream size, elevation, and stream slope, we demonstrate a positive response of riparian area vegetation to conservation-oriented grazing approaches and livestock exclosures, extensive beaver dam development, increased precipitation, and lack of wildfire. We show that livestock management which emphasizes riparian recovery objectives can be an important precursor to beaver activity and describe 11–39% increases in floodplain vegetation productivity where conservation-oriented grazing approaches or livestock exclosures and high beaver activity occur together on low-gradient sites. Land management decisions can therefore potentially confer resiliency to riparian areas under changing and variable climate conditions–the increased vegetation productivity resulting from conservation-oriented grazing or exclosures and high amounts of beaver activity at our sites is the equivalent to moving conventionally-grazed, low-gradient sites without beaver up at least 250 m in elevation or increasing water year precipitation by at least 250 mm.

Introduction

Riparian and aquatic habitats within stream corridors support a diverse array of fish and wildlife taxa and environmental processes [1, 2]. The importance of riparian and aquatic habitats

for biodiversity is often disproportionate to their overall area, especially in arid and semi-arid ecosystems where the narrow ribbon of productivity in and along streams stands in stark contrast to xeric uplands. In these systems, isolated and scarce riparian and aquatic habitats can provide seasonal or year-round habitat for a majority of terrestrial [3] or avian [4] taxa and host endemic and imperiled aquatic taxa [5, 6].

The use of riparian and freshwater habitats in drylands by fish and wildlife taxa is associated with specific attributes of those habitats. For example, in the Great Basin of the interior western United States, greater sage-grouse (*Centrocercus urophasianus*) use of riparian systems during the brood-rearing period requires the presence of high-quality forage of forbs, succulent vegetation, and insects [7, 8]. Trout of the interior western US (*Oncorhynchus* spp.) have been linked to cool stream temperatures [9–11] and the presence of woody streamside vegetation [11, 12]. Many of the aquatic and riparian habitat conditions required by fish and wildlife can be degraded by the individual and synergistic effects of disturbances in dryland ecosystems, which include wildfire [8,13–16], drought [16–18], flooding [13, 19], and livestock grazing [20, 21].

Controls on discrete wildfire, flood, and drought events in dryland ecosystems occur at regional or global scales. For example, drought and flooding in drylands can be associated with global climate variability, such as the El Niño-Southern Oscillation [22, 23], while wildfire can be linked to regional climate [24, 25] and vegetation dynamics, including invasion of non-native grasses [26, 27]. In contrast, livestock grazing is controlled at local scales through the decisions of land managers and potentially represents a chronic disturbance, especially where concepts of managed grazing are not specifically implemented [28].

Livestock can alter the amount, structure, and community composition of vegetation within riparian areas through consumption, selection, and trampling. These alterations to vegetation remove important drivers of stream morphology, from channel-forming large wood to bank-stabilizing roots, while the compaction and shear of livestock hooves alters the physical form of floodplains [20, 21] and reduces riparian habitat quality for wildlife [29, 30]. For instream habitats, unmanaged livestock grazing may be associated with decreased habitat quality for aquatic taxa in the form of decreased streambank stability, higher concentrations of fine sediments, decreased riparian vegetation, and altered food webs [20, 31–34]. The legacy effects of livestock grazing in riparian systems can persist long after livestock use has ended [35].

To enhance the resistance and resiliency of streams and riparian areas to wildfire and drought and in response to known impacts of livestock, land managers increasingly use conservation-oriented grazing strategies to mitigate impacts to vegetation, biodiversity, and hydrology within the stream corridor and to restore proper riparian function [36]. These strategies attempt to balance grazing periods with opportunities for plant growth by adjusting grazing season, duration, and intensity, and often include a combination of tools and techniques designed to improve livestock distribution and reduce use of riparian areas [28, 36]. Examples of practices that promote rather than impede recovery include altering the timing of cattle use to outside the growing season (i.e., spring or fall), limiting duration or intensity of use within seasons, resting pastures during some years, using rotation among pastures, and excluding some areas from use completely. Common examples of tools and techniques which improve livestock distribution and management include offsite water developments, fencing, use of supplements such as salt blocks, and implementing herd management and animal husbandry practices such as herding and riding, culling, and changing class of livestock [28, 36].

Concurrently, in dryland ecosystems within the native distribution of North American beaver (*Castor canadensis*) there is increasing awareness among land managers of the role of beaver, beaver dams, and beaver dam analogues as restoration tools in degraded riparian systems

[37–40]. In arid and semi-arid landscapes, beaver dams increase water storage in streams and in adjacent floodplains, maintain water within the river course, and promote riparian vegetation [41]. Active and abandoned dams are associated with elevated structural and thermal heterogeneity of instream habits [42–46] and increased woody vegetation in riparian habitats [47]. Gibson and Olden [41] provide a thorough review of the response of hydrology, geomorphology, water quality, riparian vegetation, and wildlife to the habitat manipulations of beaver.

As land managers implement conservation grazing strategies and beaver restoration approaches, monitoring how habitats are affected by these treatments can be challenged by the long time horizon and variability in response. Archives of remote sensing data provide an opportunity to efficiently and effectively monitor the response of riparian vegetation to disturbances and management treatments over decadal time horizons [48, 49]. Satellite and aerial imagery are well-suited for monitoring riparian vegetation productivity and trend in dryland ecosystems due to the quality and time series of remotely-sensed data products, the seasonal and structural contrast between riparian areas and adjacent uplands, and the logistical challenges of field monitoring in undeveloped landscapes [50]. Satellite-derived measures of vegetation productivity, such as the normalized difference vegetation index (NDVI), use multispectral information to estimate the amount and vigor of green vegetation [51]. Higher resolution aerial imagery (as captured by planes or drones) has been used for identifying specific features of riparian areas, such as dewatered channels [52], density of vegetation [53], and individual beaver dams [54].

In this study, we used remote sensing datasets to evaluate changes in riparian productivity in five semi-arid watersheds due to changes in livestock grazing regimes, while also accounting for the environmental setting created by stream characteristics as well as other ecosystem changes due to beaver colonization, wildfire, and climate variability. Our objectives were to 1) assemble a unique dataset of vegetation productivity, digitized beaver dam locations, and grazing histories spanning three decades; 2) apply a linear mixed modelling approach to evaluate biotic and abiotic predictors of riparian vegetation productivity and quantify anticipated gains in productivity in response to management decisions; and 3) use path analysis to evaluate direct and indirect linkages between biotic and abiotic factors and describe the restoration pathways of riparian vegetation in response to management strategies. Our study uses extensive archives of satellite and aerial imagery and leverages new developments in cloud-based remote sensing to facilitate rapid analysis of long-term datasets.

Methods

Study area

Our analysis area includes Susie Creek (116˚W, 41˚N), Jakes Creek (115˚W, 41˚30'N), and South Fork Salmon Falls Creek (115˚W, 41˚45'N) in Nevada and Willow Creek (118˚15'W, 42˚10'N) and Whitehorse Creek (118˚W, 42˚10'N) in Oregon (Fig 1). All watersheds are in the Northern and Central Basin and Range ecoregions in the western United States [55] and within the floristic Great Basin (hereafter Great Basin). Climate at all sites is characterized by hot, dry summers and cold, moist winters [55] which results in hydrologic regimes with peak flows associated snowmelt and rain in spring and low baseflow during summer [56]. Average elevation ranges from 1,750 m in Willow Creek to 2,100 m in South Fork Salmon Falls Creek. Vegetation along streams and on mesic sites is dominated by native taxa and includes aspen (*Populus tremuloides*), black cottonwood (*Populus balsamifera*), willow (*Salix* spp.), and thinleaf alder (*Alnus incana*) at higher elevations and a variety of willows, sedges (*Carex* spp.), rushes (*Scirpus* and *Eleocharis* spp.), and riparian grasses and forbs at lower elevations.

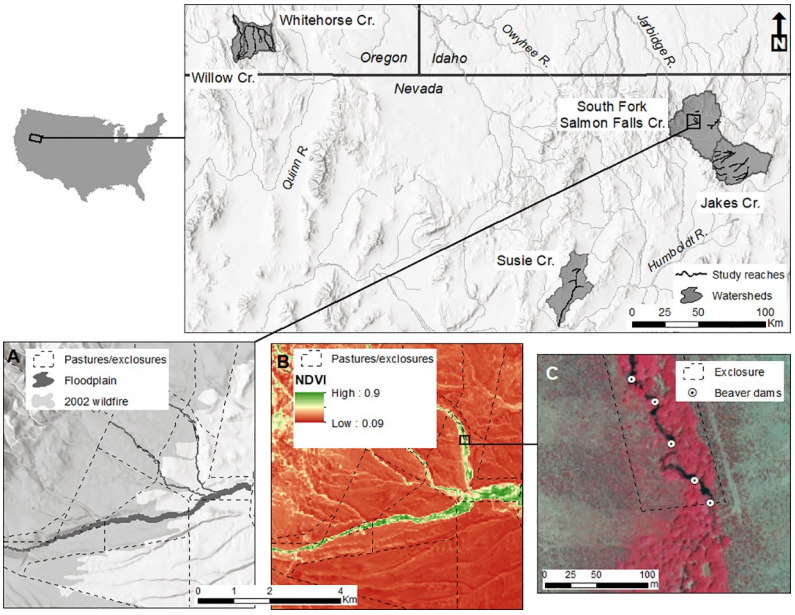


Fig 1. Locator map, observation units, and imagery examples. Top panels: Location of study watersheds. Panel A: Example of observation units, delineated by pasture or exclosure, modeled floodplain boundaries, and individual streams, with example wildfire boundary overlaid. Panel B: Example maximum growing season NDVI measured from Landsat 8 in 2015. Panel C: Example beaver dam locations identified in 2015 false-color National Agriculture Imagery Program (NAIP) imagery within an exclosure and adjacent pasture area. Landsat imagery is reprinted from US Geological Survey and NAIP imagery is reprinted from USDA Farm Service Agency, both under a CC BY license (public domain).

https://doi.org/10.1371/journal.pone.0208928.g001

Sagebrush (*Artemisia tridentata*) and a variety of perennial bunchgrass species dominate the uplands. All sites provide riparian or aquatic habitat for at least one imperiled or sensitive taxa, including greater sage-grouse, Great Basin distinct population segment of Columbia spotted frog (*Rana luteiventris*), Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*), and Columbia River redband trout (*Oncorhynchus mykiss gairdneri*).

Land managers in each watershed have implemented conservation-oriented grazing management at various times during recent decades with an objective to improve riparian conditions and habitat for imperiled or sensitive fish and wildlife. Each watershed contains rangelands administered by US Bureau of Land Management (BLM), US Forest Service, and private landowners within grazing allotments comprised of pastures and exclosures. Livestock management plans developed for allotments define seasons of use, stocking rates, and pasture and exclosure boundaries, and often include specific riparian habitat goals. In some cases, managers implemented temporary closures or restrictions in grazing use to mitigate the effects of wildfire. Beaver have expanded their habitat use in each watershed over the last thirty years through natural colonization and without the aid of any specific wildlife management strategies (e.g., trapping limits or translocation).

Wildfires and climate variability have affected the study watersheds over the three decades: five wildfires have affected riparian areas in the watersheds, and water year precipitation has varied up to 125% from year to year (S1 Dataset). Of the five watersheds in the study, only Susie Creek includes a streamflow gage. There, peak water year flows from 1993–2015 ranged from 0.34–45 cms and mean water year flows ranged from 0.014–0.97 cms (S1 Dataset); these streamflow metrics moderately correlate with water year precipitation (Pearson correlation coefficient = 0.70 and 0.61, respectively).

Observation unit delineation

In each study watershed we created observation units (analogous to sites) based on the riparian area of individual streams within pasture or exclosure boundaries. Within each drainage, we delineated riparian areas for named streams in the National Hydrography Dataset (NHD; [57]) using the Valley Bottom Extraction Tool (V-BET; [58]) and a 10-m resolution digital elevation model [59] using a GIS software (ArcGIS 10.5—ESRI, Inc.). The V-BET tool identifies a variable-width floodplain based on stream size attributes and terrain characteristics such as slope. We then intersected the riparian area with the local catchment area of each stream reach and pasture or exclosure boundaries [60, 61] to create our final observation units. The final units represent the floodplain area of each unique combination of named stream, Strahler stream order, and pasture or exclosures (e.g., the 2nd order section of Doolittle Creek in the 15 Mile pasture). These units allowed us to characterize the effect of grazing treatments on riparian vegetation within observation units, while controlling for environmental variability within pastures or exclosures associated with stream characteristics (e.g., streamflow, slope, elevation).

Riparian vegetation productivity

We used a 31-year historical archive of seasonal peak NDVI measurements from Landsat satellite imagery as a response variable and estimate of annual riparian vegetation productivity. NDVI is a remotely-sensed measure of active photosynthesis and vegetation productivity widely used to track vegetation dynamics in response to environmental and land management changes [48, 62, 63]. NDVI is commonly used as a proxy for vegetation condition as related to factors such as leaf area, vegetation cover, and net primary productivity [64].

We generated annual maps of maximum-value composite NDVI for the late growing season (late July–mid-September) from US Geological Survey Landsat 5, 7, and 8 Collection 1 Tier 1 surface reflectance products ([65]; 30 m^2 pixel resolution, typically 6 Landsat scenes per late growing season) using Google Earth Engine [66], and summarized the average value within each observation unit for each year from 1985–2015. We used a maximum-value composite ("greenest pixel") approach to minimize phenological differences across observation units [62] and focused on late growing season NDVI to minimize the influence of annual grasses and other vegetation outside of the riparian area, which senesce by mid-summer [67]. We also calculated an annual measure of the proportion of each observation unit with at least one valid NDVI pixel value (i.e., not identified as cloud cover, shadow, snow, or water in Landsat Collection 1 Pixel QA band attributes) for the late growing season and excluded any observation unit with an average value less than 0.5. For Landsat 8 NDVI data, we applied the function described by Roy and others [68] to adjust for comparison with Landsat 5 and 7.

Spatial covariates

We selected a set of spatial covariates for predicting riparian vegetation productivity in observation units based on a literature review of influences on riparian vegetation and the availability of datasets for the study areas. The final list of covariates includes a mix of continuous and categorical datasets, observation unit-scale and watershed scale-data, and data with and without a temporal component (Table 1). For predicting annual riparian vegetation productivity in observation units, we summarized covariates for each observation unit for each year. Where observation unit-scale data were lacking, we applied watershed-scale data to all observation units in the watershed; where temporal data were lacking, we applied an identical value to all observation units for all years.

Table 1. Spatial covariates used to predict riparian vegetation productivity.

Variable	Definition	Temporal and spatial scale	Data source
Livestock grazing regime	Categorical measure of livestock use (conservation, exclosure, or conventional); classified as "Conservation" if listed in Swanson et al. 2015, Table 2 as supporting riparian functions and allowing recovery	Category by year (1985–2015) for each observation unit	BLM [60, 61]
Beaver dams	Continuous measure of beaver use of stream as dams per stream km	Density by year for each observation unit; limited availability, see Table 3	See Table 3
Wildfire	Categorical measure of wildfire or wildfire recovery (unburned, burned); classified as "Burned" for 2 years following wildfire if at least 1/3 of observation unit overlaps with wildfire boundary	Category by year (1985–2015) for each observation unit	MTBS Burned Areas Boundaries Dataset [69]
Precipitation	Continuous measure of total water year precipitation in dm	Sum of daily precipitation from Oct 1 of previous year to Sept 30 for each year (1985–2015) by watershed; same value applied to all observation units in watershed	Daymet V2 [70] (1 km^2 resolution)
Drought	12—month Evaporative Demand Drought Index (EDDI)	12-month EDDI for Aug 1 for each year (1985–2015) by watershed; same value applied to all observation units in watershed	EDDI Map Archive [71] (12 km^2 resolution)
Stream size	Continuous measure of upstream contributing watershed area in km^2	Value for each observation unit; not temporal–same value applied to all years	NHD-Plus [72]
Stream slope	Continuous measure of stream slope as %	Value for each observation unit; not temporal–same value applied to all years	Max.—min. elevation on stream from 10-m DEM [59]/stream length from NHD [57]
Elevation	Continuous measure of average stream elevation in km	Value for each observation unit; not temporal–same value applied to all years	10-m DEM [59]

https://doi.org/10.1371/journal.pone.0208928.t001

Livestock grazing alters the amount, structure, and community composition of riparian vegetation [20], while conservation-oriented grazing regimes and livestock exclosures can facilitate riparian vegetation recovery [28]. We compiled grazing histories dating to at least 1985 (the first year with satellite imagery at 30 m^2 resolution) for all observation units based on BLM records and grazing plans. We characterized grazing regime for each unit by year as "conservation-oriented," "exclosure," or "conventional." Conservation-oriented grazing regimes support riparian function and allow recovery after use and include strategies such as short grazing periods, long post-grazing recovery periods, periods of rest, and explicit riparian objectives [28]. Exclosures are fenced areas built to exclude livestock completely and include both reference exclosures (linear features on low-gradient stream channels in alluvial basins) and protective exclosures (features focused on areas of specific concern, including springs) [73]. Although we consider exclosures to be a conservation strategy, these areas were considered separately from conservation-oriented grazing treatments. Conventional livestock grazing practices include grazing throughout the growing period with little or no effort to control amount, duration, or distribution of livestock use in specific areas [36] and tend to preclude recovery of riparian areas. Land managers largely initiated the switch from conventional grazing to conservation-oriented grazing in 1985 and 1996 in South Fork Salmon Falls Creek, in 1989 in Willow and Whitehorse Creeks, in 1992 and 2007 in Susie Creek, and in 2001 in Jakes Creek, although timing varied by pasture. Grazing strategies for each watershed are described in more detail in existing literature [28, 74–76].

Beaver can create increased hydrological connectivity and water storage in floodplains through dam construction, which can have a positive effect on floodplain vegetation productivity [41]. Despite consuming and cutting vegetation, beaver can promote riparian vegetation biomass and vigor [77]. To characterize the density of beaver dams within observation units, we digitized the locations of individual dams visible within aerial photographs. Source imagery

Table 2. Imagery used to identify beaver dams.

Year	Willow	Whitehorse	SF Salmon Falls	Jakes	Susie	Imagery resolution (m^2)
1986			BLM CIR (3)			0.1
1991					BLM color (0)	0.1
1994	DOQ B&W (0)	DOQ B&W (9)	DOQ B&W (14)	DOQ B&W, BLM color (18)	DOQ B&W (0)	1
1998					BLM CIR (25)	0.4
2000	DOQ B&W (14)	DOQ B&W (11)				1
2005	NAIP 3-b (25)	NAIP 3-b (25)				0.5
2006			NAIP 3-b (23)	NAIP 3-b (45)	*NAIP 3-b (32)*	1
2009	NAIP 4-b (88)	NAIP 4-b (42)				0.5
2010			NAIP 4-b (46)	NAIP 4-b (32)	NAIP 4-b (137)	1
2011	NAIP 4-b (42)	NAIP 4-b (33)				1
2013			NAIP 4-b (104)	NAIP 4-b (42)	NAIP 4-b (156)	1
2014	*NAIP 4-b (37)*	*NAIP 4-b (39)*				1
2015			NAIP 4-b (176)	NAIP 4-b (57)	NAIP 4-b (245)	1

BLM CIR = Bureau of Land Management low elevation color infrared imagery; BLM color = Bureau of Land Management low elevation color imagery; DOQ B&W = Black and white digital orthophoto quadrangle; NAIP 3-b = National Agriculture Imagery Program true color imagery; NAIP 4-b = true color imagery with infrared band. Count of beaver dams observed in imagery in parenthesis. Italics indicate imagery which capture a wildfire recovery period.

https://doi.org/10.1371/journal.pone.0208928.t002

included single frame historical true-color or false-color aerial photos from BLM or US Geological Survey Earth Explorer archives which required georeferencing, and more contemporary digital, georeferenced black and white (digital ortho-quadrangles) and 3- and 4-band National Agricultural Imagery Program images (Table 2). All imagery had a spatial resolution of 0.4–1 m^2. We used a consistent map scale for digitizing: 1:2,500 for the finer resolution imagery and 1:5,000 for the coarser resolution imagery. We are unable to determine through aerial imagery interpretation if beaver dams are active or abandoned, and therefore cannot estimate the degree to which sites are actively "managed" by beaver through herbivory, dam construction and repair on an annual basis. Nonetheless, riparian vegetation is likely benefiting from the presence of beaver dams where beaver are absent by virtue of floodplain saturation and water storage [41].

Wildfire can consume riparian vegetation [78]; to characterize fire effects within observation units, we calculated the proportion of each observation unit which overlapped with a wildfire identified in the Burned Areas Boundaries Dataset [69] for each year from 1985–2015. We categorized an observation unit as burned and recovering ("Burned") for two years if at least one-third of an observation unit overlapped with a wildfire boundary. We selected a two-year recovery period based on preliminary data exploration for our sites; riparian vegetation in Great Basin sites can rapidly recover from wildfire through basal sprouting and recruitment of seeds and vegetative propagules distributed by streamflow [78]. We determined which two years received the "Burned" designation based on the satellite imagery: if the satellite record for the late growing season included a pre-fire observation, the observation unit was considered "Burned" for the two years following the year of the fire; if the satellite record did not include a pre-fire observation, then the observation unit was considered "Burned" for the year of the fire and following year. We characterized all other years as "Unburned."

Annual growth and vigor of riparian vegetation is linked to annual precipitation [18, 48]. Annual precipitation increases riparian water availability through higher soil moisture and drives many key seasonal streamflow characteristics (peak flow, low flow, base flow), which affect riparian vegetation growth, dispersal, and structure [1, 79–82]. To account for annual

climate variability related to precipitation, we summed daily precipitation values in the Daymet V2 dataset [70] for each water year (October 1 of the prior year through September 30 of year of interest) for each year from 1985–2015 at the geometric centroid of each watershed. We used water year to capture fall and winter snowfall which does not contribute to streamflow until the following spring. Due to the lack of streamflow gage data for each study watershed, we used water year precipitation as a proxy for streamflow; peak water year streamflow and mean water year streamflow are moderately correlated with water year precipitation in Susie Creek (Pearson correlation coefficient = 0.70 and 0.61, respectively, for 1993–2015), the only study watershed with a streamflow gage.

Sustained drought affects vegetation productivity by amplifying soil moisture supply limitations through atmospheric water demand [49, 83]. To account for climate variability related to drought, we summarized the Evaporative Demand Drought Index (EDDI) for a 12-month period ending Aug 1 for each year from 1985–2015 at the geometric centroid of each watershed. EDDI accounts for moisture, wind speed, solar radiation, and temperature on the land surface and in the atmosphere to characterize sustained and acute periods of drought [83, 84]; positive EDDI values indicate periods of high evaporative demand and potential for drought. The 12-month EDDI reveals sustained drought stress; while other time scales of precipitation or EDDI may be better predictors of NDVI, comprehensive evaluation of different periods was beyond the scope of this analysis.

We calculated a set of static covariates (i.e., those lacking a temporal component) related to stream characteristics within observation units, including stream size, stream slope, and elevation, using NHD-Plus [75], NHD [60], and a 10-m digital elevation model [62]. The stream size covariate captures within-watershed variability of streamflow when considered with precipitation in absence of reach-scale streamflow data [85]. Seasonal flows affect riparian vegetation growth, dispersal, and structure [1, 79–82]. Stream slope determines floodplain form (e.g., depositional vs. erosional environments) and thus riparian vegetation potential [1, 79, 80, 86]. The elevation covariate captures variability of vegetation communities and productivity along elevation gradients [79] and serves to account for the variability of watershed-scale precipitation within observation units.

Statistical analysis

We evaluated the influence of grazing regime and beaver colonization on riparian vegetation productivity while accounting for other important temporal and spatial factors using linear mixed models (LMM). We fit several candidate LMMs, which are essentially multiple regression models with a random effect, to the data and evaluated them in a model selection framework. We used average peak annual NDVI within observation units as a response variable, and evaluated grazing regime, beaver dam density, water year precipitation, drought, wildfire, elevation, stream size, and stream slope as predictor variables. We used pasture by watershed as a random effect and grazing management (categorical: Conventional, Conservation, Exclosure) and wildfire (Unburned = 0; Burned = 1) as treatments (fixed effects). Candidate models were constructed of all combinations of predictor variables with the constraint that EDDI and precipitation could not be in the same model due to their correlation (r = -0.604). We hypothesized positive relationships between NDVI and beaver dam density, precipitation, elevation, and stream size due to increased water availability. We hypothesized negative relationships between NDVI and conventional grazing, EDDI, wildfire, and stream slope due to removal of plant biomass by grazers and wildfire, decreased water availability for vegetation under drought conditions, and poorly defined and highly dynamic floodplains along higher gradient streams. We also evaluated the interaction of slope and beaver dam density due to the potential

differences in the effect of beaver on vegetation productivity in high vs. low slopes due to increased impoundment size and floodplain connectivity in low slope areas [87], as well as the interaction of grazing regime and beaver dam density due to the potential competition between cattle and beaver for woody vegetation forage [88]. Candidate models were constructed using all combinations of variables and fit to the data, and model plausibility was determined using Akaike's Information Criterion for small sample size [89]. Candidate models within 4 AICc units of the best model (minimum AICc) were considered plausible. Fit of the most plausible regression model was evaluated using both the marginal and conditional R^2 [90].

We also used path analysis as a complement to the linear mixed model analysis to evaluate the association of riparian vegetation productivity with grazing regime, beaver dam density, wildfire, climate, and stream characteristics, as well as test for explicit linkages between those factors. Path analysis is an extension of multiple regression that estimates the magnitude and significance of direct and indirect relationships between sets of observed variables while accounting for their covariance, and it produces a directed graph (path diagram or model) that shows these inter-relationships [91]. Path analysis is often thought of as more confirmatory of causal relationships than other statistical modelling approaches [92]. We developed a conceptual model of the relationships among significant predictor variables identified in the LMM to inform our initial path analysis. For the path analysis, we reconfigured grazing regime into a continuous variable that was the sum of the main and interaction parameter estimates from the multiple regression model (Conventional = 0; Conservation = 0.030; Exclosure = 0.043). This allowed us to keep the path analysis simple instead of duplicating relationships associated with two separate factors (i.e., as Typical = 0, Conservation = 1; and Conventional = 0 and Exclosure = 1) when the general relationships were expected to be identical. In addition to direct linkages between each predictor variable and NDVI, the model also includes a hypothesized link between beaver dams and precipitation and stream characteristics such as stream size, slope, and elevation to reflect geomorphic and streamflow controls affecting beaver dam placement and permanence [87]; between precipitation and wildfire to reflect the association between drought years and fire [24, 25]; and between grazing regime and beaver dam density reflecting the potential for conventional grazing to limit woody vegetation, a key source of dam construction materials and food for beaver [77, 88]. The initial path model was fit using the lavaan package in R (R Core Team 2015; [93]), and the semPaths function was used to display the directed graph [94]. We used standardized coefficients to examine the significance of each pathway using $p < 0.05$.

Results

We delineated 93 unique observation units (average size = 0.2 km^2, min = 0.01 km^2, max = 1.6 km^2, total = 21.5 km^2) and summarized riparian productivity, grazing information, climate, and wildfire for each over 31 years, representing 2,883 total observations. NDVI ranged from 0.10 to 0.70 across all observation units and years; observation units with conventional grazing had average peak NDVI values of 0.27, while units with exclosure or conservation-oriented grazing averaged 0.35 and 0.34, respectively. Of the total observations, we used 541 for the statistical analysis: these observations occurred during the 13 years where high-resolution aerial imagery was available for identifying beaver dams; each watershed had 5 to 7 years of high-resolution imagery available with an average lag of 4.5 years between observations (min. = 2, max. = 12; Table 2). By watershed, the final available observations total 106 for 6 years in South Fork Salmon Falls Creek, 105 for 5 years in Jakes Creek, 84 for 7 years in Susie Creek, 168 for 6 years in Whitehorse Creek, and 78 for 6 years in for Willow Creek.

We identified 1,510 beaver dams in 27 aerial imagery datasets. These dams occurred at 1,083 unique locations, and 28% of locations had persistent dams which occurred in multiple imagery sets. Multiple dams in multiple watersheds appear to have persisted for over 15 years. The greatest density of beaver dams identified within an observation unit was 10 dams on 0.47 km of stream within an exclosure on Willow Creek in 2009. The largest number of dams observed in a watershed within a single year was 245 on 59.5 km of stream in Susie Creek in 2015. The number of dams increased in all watersheds between the first and last imagery dates (Table 2).

Wildfire occurred in four watersheds and included the Camp Creek Fire of 2000 in South Fork Salmon Falls Creek, the Basco and Suzie Fires of 2006 and Camp Creek fire of 2007 in Susie Creek, and the Holloway Fire of 2012 in Willow and Whitehorse Creeks. We attributed all observation units as burned for the year of the fire and the following year except for those within the Holloway Fire boundary, which burned in August after pre-fire satellite imagery had been collected and were attributed as burned for the 2 years following the fire. Limited availability of aerial images for characterizing beaver dam densities constrained our evaluation of wildfire effects to the Susie, Willow, and Whitehorse Creek watersheds.

As we hypothesized, the linear mixed models revealed a positive relationship between riparian productivity and conservation-oriented grazing or exclosure, beaver dam density, precipitation, and stream size, and a negative relationship between riparian productivity and stream slope and recent wildfire. Model selection showed only four plausible models ($\Delta AIC_c \leq 4$; Table 3). The strongest Pearson correlation among candidate spatial covariates was $r = 0.604$ between precipitation and EDDI, which were never included in the same candidate models; this suggests that multicollinearity was not an issue in any candidate model. Of all variables evaluated, EDDI was not in any plausible model, and stream size and the beaver x grazing interaction were each in only two of the top four plausible models (Table 3). We interpreted the most plausible candidate model in the top set without the beaver x grazing interaction term (third most plausible model) because the interaction term had little effect on the log-likelihood and appeared to be uninformative [95], exploratory analysis showed large uncertainty in parameter estimates for interaction terms (S1 Fig), and there were very few beaver dams under conventional grazing (Fig 2). The interpreted model fit the data well (marginal $R^2 = 0.29$; conditional $R^2 = 0.83$).

Standardized parameter estimates from the fitted model showed that conservation-oriented grazing and exclosures had similar positive effects on NDVI (Table 4). NDVI was significantly higher under conservation-oriented grazing and exclosures vs. conventional grazing ($p < 0.001$; Table 4), but there was no significant difference between the effect of conservation-

Table 3. Candidate models explaining how spatial covariates influence riparian vegetation productivity (NDVI).

Candidate models	df	logLik	AICc	ΔAICc	w_i
BeaverxSlope +BeaverxGraze + Elev + Fire + Size + Precip	14	-365.7	760.15	0.0	0.38
BeaverxSlope +BeaverxGraze + Elev + Fire + Precip	13	-367.0	760.67	0.5	0.29
BeaverxSlope + Graze + Elev + Fire + Size + Precip	12	-368.6	761.71	1.6	0.18
BeaverxSlope + Graze + Elev + Fire + Precip	11	-370.1	762.63	2.5	0.11
BeaverxSlope +BeaverxGraze + Elev + Fire + Size + Precip	13	-369.6	765.96	5.8	0.02
BeaverxSlope +BeaverxGraze + Elev + Fire + Precip	12	-370.9	766.32	6.2	0.02
Beaver + Slope +BeaverxGraze + Elev + Fire + Size + Precip	11	-374.6	771.71	11.6	0.00
Beaver + Slope +BeaverxGraze + Elev + Fire + Precip	10	-376.1	772.57	12.4	0.00

Only models with ΔAICc < 15 are shown, and all models with an interaction term also had main effect terms. df = degrees of freedom; logLik = Log-likelihood; wi = Akaike weights

https://doi.org/10.1371/journal.pone.0208928.t003

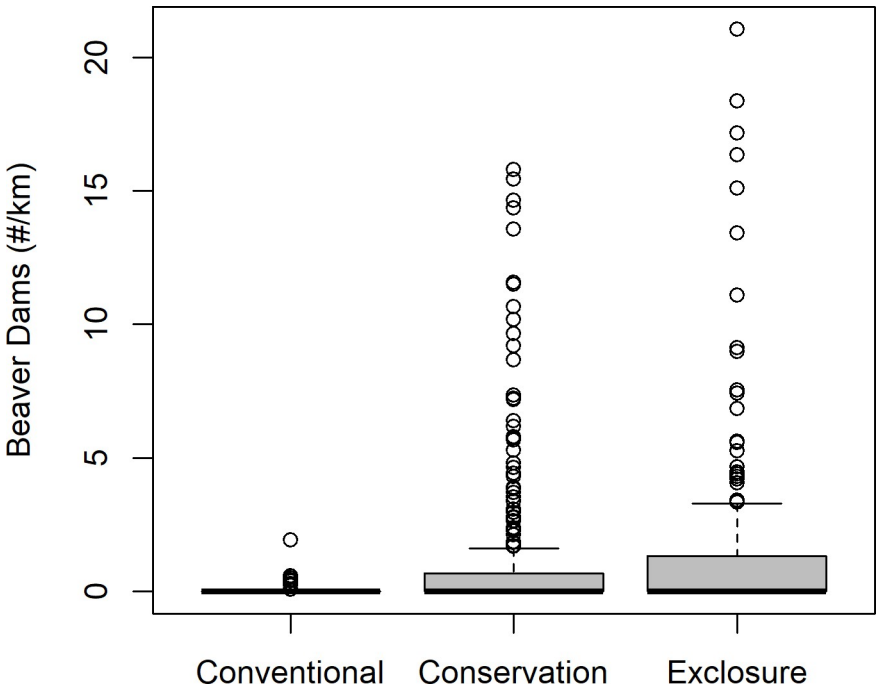


Fig 2. Beaver dam density by grazing treatment.

https://doi.org/10.1371/journal.pone.0208928.g002

oriented grazing and exclosure on NDVI (t = 0.841; p = 0.401). Beaver had a positive effect on NDVI but only on low-gradient streams, as indicated by the interaction between beaver dam density and stream slope. While the effect of beaver was independent of grazing treatment in the interpreted model, there were very few beaver dams under conventional grazing (Fig 2). The un-standardized parameter estimates provide a means to characterize the gains in riparian productivity in our study watersheds created by conservation grazing and beaver management relative to sites with conventional grazing and without beaver. Our models indicate an expected increase in NDVI of 25% (± 14% 2 SE) with livestock exclosures and high beaver dam densities (i.e., 2 beaver dams/km) and 20% (± 7% 2 SE) with conservation-oriented

Table 4. Parameter estimates and p-values from a multiple regression model predicting NDVI.

	Un-standardized		Standardized		
Parameter	b_i	**2 SE**	b_i	**2 SE**	**p-value**
Intercept	-0.149	0.175	-0.174	0.247	0.158
Precipitation (dm)	0.021	0.003	0.262	0.038	<0.001
Fire (Unburned = 0; Burned = 1)	-0.039	0.014	-0.372	0.132	<0.001
Elevation (km)	0.214	0.093	0.389	0.169	<0.001
Grazing: Conservation (Conventional = 0; Conservation = 1)	0.030	0.013	0.282	0.123	<0.001
Grazing: Exclosure (Conventional = 0; Exclosure = 1)	0.043	0.032	0.403	0.302	0.008
Stream size (km^2)	0.021	0.024	0.097	0.111	0.082
Beaver dam density (#/km)	0.012	0.003	0.146	0.061	<0.001
Slope (%)	-0.012	0.007	-0.267	0.117	<0.001
Slope x Beaver	-0.003	0.002	-0.146	0.083	<0.001

Standardized parameter estimates are scaled and centered. 2 SE = 2 standard errors.

https://doi.org/10.1371/journal.pone.0208928.t004

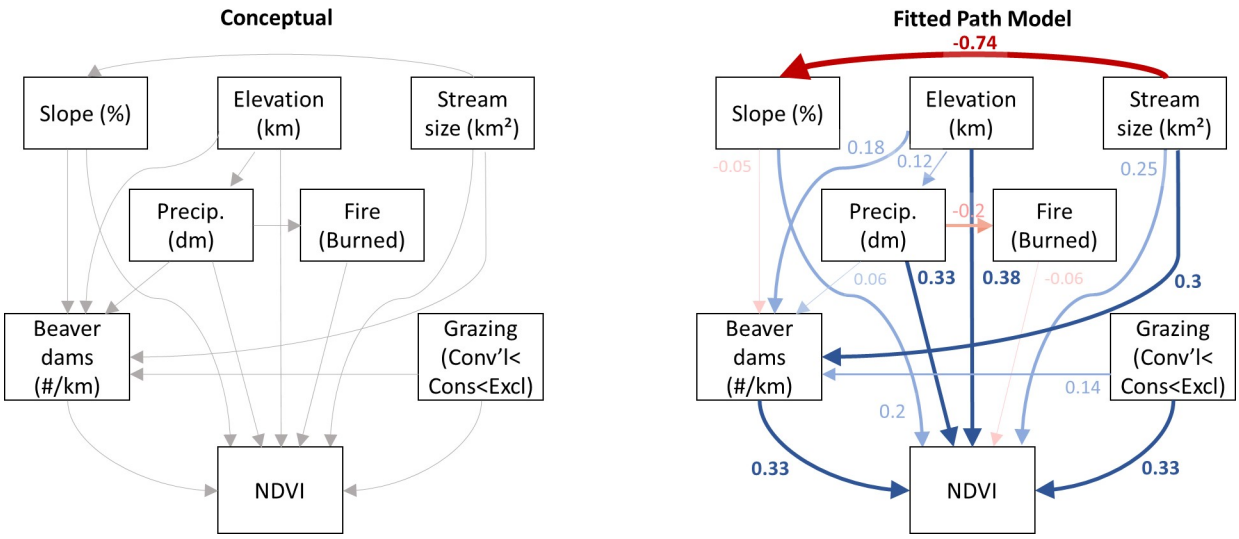


Fig 3. Conceptual and fitted path models. Fitted path model only shows effects with $p < 0.05$. Blue lines in the fitted model indicate positive effects, and red lines indicate negative effects. Values indicate standardized path coefficients; values around 0.3 are interpreted as moderate effects, while values around 0.1 are interpreted as weak effects.

https://doi.org/10.1371/journal.pone.0208928.g003

grazing and high beaver dam densities, based on an average NDVI of 0.27 across the 31-year period for all observations units with conventional grazing and no beaver present.

Path analysis showed direct and indirect linkages between riparian productivity, grazing management, beaver density, climate, and stream characteristics in both shared and contrasting ways with the linear mixed modelling approach. Model fit was acceptable based on the comparative fit index (cfi = 0.954; root mean squared error approximation = 0.081). The effect of slope on beaver dam density ($p = 0.282$) and wildfire on NDVI ($p = 0.083$) were non-significant at $\alpha = 0.05$. The fitted model demonstrated a direct effect of high water year precipitation, high beaver dam densities, and high elevations on high riparian productivity (Fig 3). High beaver dam densities are associated with larger streams, confirming the mediating effect of stream characteristics on beaver dam density. Conservation grazing approaches have moderate direct and weak indirect effects on high riparian productivity; indirect effects occur as grazing management is linked to increased beaver dam densities, which directly affects riparian productivity. Wildfire is associated with lower water year precipitation amounts. Large stream size is also directly linked to high riparian productivity; however, the linkage is weak.

Fig 4 demonstrates the generalized progression of recovery in the systems we studied using a 3-decade riparian area NDVI time series for a single Susie Creek pasture. First, removal or reduction in grazing pressure during the growing season allows for the rapid establishment or recovery of woody streamside vegetation within 3 years. Beaver then colonize or expand their habitat use to take advantage of the woody vegetation, especially willow. As beaver populations increase, additional dam building activity enhances floodplain inundation, facilitating additional riparian vegetation productivity. Wildfire can reduce this recovery, but the effects are only temporary.

Discussion

Multiple sensitive taxa depend on riparian areas within the Great Basin, and land managers are increasingly using livestock grazing management and restoration techniques involving beaver reintroduction or beaver dam analogues to improve riparian area condition and function [28, 36–39]. Response of riparian area vegetation to these treatments can occur at variable

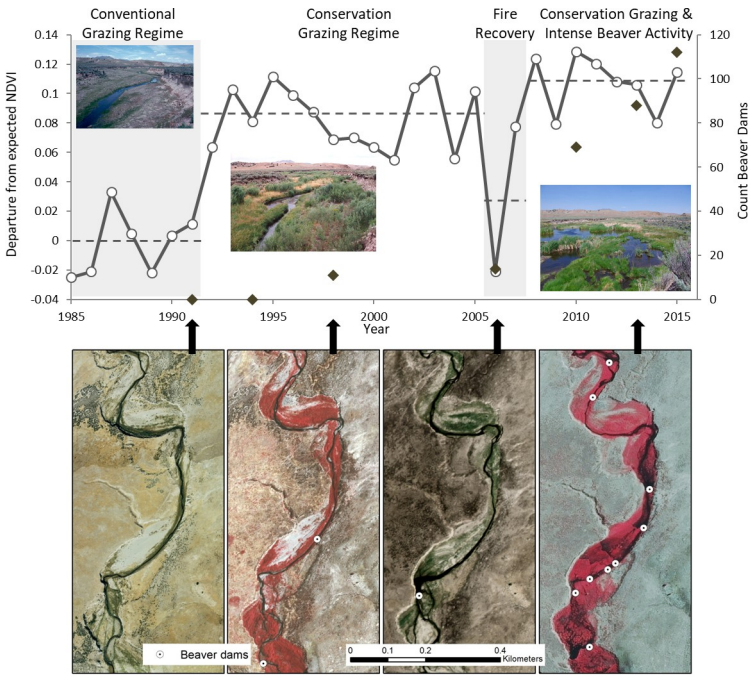


Fig 4. Time series of riparian vegetation recovery. Top panel: Departure from expected NDVI under conventional grazing regimes and 0 beaver (solid line, left y-axis) and beaver dam count (diamonds, right y-axis) time series data for the Susie Creek riparian pasture in the Carlin Field allotment. Departure from expected NDVI by year is represented using each year's residual from the linear relationship between NDVI and water year precipitation for Susie Creek watershed observation units with conventional grazing regime, no wildfire effects, and 0 beaver dam observations. Negative departure values indicate lower than expected NDVI values given that year's precipitation; positive values indicate higher than expected NDVI. Average NDVI departure for 4 treatment and condition periods shown with dashed lines. Bottom panel: Example aerial photos from a portion of the pasture from 1991, 1998, 2006, and 2013 showing riparian vegetation extent and beaver dams. Aerial photos are reprinted from USDA Farm Service Agency and site photographs are reprinted from US Bureau of Land Management, both under a CC BY license (public domain).

https://doi.org/10.1371/journal.pone.0208928.g004

rates and can be influenced by disturbances such as drought and wildfire, making it difficult to parse out the effects of management actions without long-term evaluation of responses. The ability to apply remote sensing for effective long-term monitoring can improve our understanding of the interactions between grazing management and beaver and help land managers to better plan and evaluate their restoration actions within riparian areas.

Prior research has elucidated relationships between grazing management, beaver, climate, and stream characteristics individually or in tandem relative to riparian area productivity in arid and semi-arid landscapes. For example, Huntington and others [48] described the correlation between climate and riparian vegetation vigor measured as NDVI, while multiple studies have demonstrated recovery of willow and other riparian vegetation with exclosure or alternative management of livestock grazing [73, 96–99], including in adjacent watersheds [53, 100, 101]. Similarly, an increasing body of literature describes the anticipated riparian area benefits associated with beaver activity and identifies those physical and biological site conditions conducive to extensive beaver dam development [37–47, 87]. While others have described the potential mechanisms through which grazing can limit beaver and riparian recovery [77, 88, 102], our results are unique in demonstrating that grazing management which emphasizes riparian recovery objectives can be an important precursor to beaver activity, and that the productivity and vigor of riparian vegetation is amplified where these grazing approaches and beaver activity occur simultaneously.

Numerous studies suggest that the warming and drying effects of changing climate will cause riparian and aquatic organisms to shift their distributions to higher elevations [103–105], and that droughts are expected to increase in duration and severity as the climate continues to warm [106]. Riparian habitats are widely regarded as having high inherent resiliency to changing climate by virtue of their linear connectivity, elevated moisture levels, and microclimate [107–109]. By evaluating our model's un-standardized parameter estimates for grazing treatments and beaver densities relative to those for annual precipitation and elevation (Table 4), we demonstrate that beaver management and conservation-oriented grazing or exclosures can enhance the resiliency of riparian ecosystems. The average increase in NDVI achieved by exclosure and high beaver dam densities is equivalent to moving a typical site in our study up in elevation by 314 m or increasing typical water year precipitation by 316 mm, nearly half of the range of precipitation observed across all sites and years in our study. Under conservation-oriented grazing and high beaver dam densities, the equivalent gains are 254 m of elevation or 256 mm of precipitation. Grazing management which emphasizes riparian recovery objectives can therefore not only increase riparian habitat for wildlife and fish but may also partially mitigate climate warming effects and increase resiliency to climate variability.

We report beaver dam densities comparable to other dryland systems [41], but document multiple examples of beaver dams persisting at least 15 years, over twice the previously reported duration for the region [44]. The beaver dam densities we evaluated likely represent an underestimation of the number of dams present in the systems. Research in nearby portions of Oregon has described detection issues related to using aerial imagery for identifying beaver dam locations, although the issues are less pronounced in arid landscapes [54].

We confirm that immutable stream characteristics such as stream size, slope, and elevation can dictate riparian area productivity, but the effects of disturbance or restoration and recovery are also often determined by other site characteristics. For example, wildfire effects are often heterogeneous in riparian systems due to variability in fuel loads, fuel type, topographic position, and microclimate dynamics [78], which may explain why wildfire is important in our linear mixed models, but a weak predictor in the path model. Site characteristics such as soil type may further dictate the rate of riparian area recovery following changes in grazing regime [35] or cause variable responses [73], and the initial rate of vegetation recovery may be controlled by climatic conditions [110]. While grazing, wildfire, and climate represent important stressors within Great Basin riparian systems, there are other potential sources of riparian area disturbance, including altered streamflow regimes, invasive plants, and agricultural water use. These disturbances may affect the physical form of floodplains, the composition of the vegetation community, water availability, and the corresponding potential for riparian vegetation recovery and restoration [19, 111, 112].

We demonstrate that grazing management within exclosures can yield riparian area vegetation productivity comparable to those produced by conservation-oriented grazing management, and that beaver dams can increase the recovery effects of each of these grazing strategies, but other considerations may dictate which treatment land managers apply to meet riparian objectives. In practice, conservation-oriented grazing strategies may be preferable to exclosures due to ease of implementation, flexibility, and scale of impact [28, 100]. We acknowledge that our categorization of grazing management into three treatments may be overly simplistic but chose general categories to facilitate comparison across watersheds and time. Similarly, management prescriptions may not correspond with actual use; exclosures, for example, can be subject to occasional or frequent livestock use due to lack of maintenance [73].

Monitoring using satellite-derived vegetation indices may not adequately capture specific habitat attributes which are associated with livestock use, meaningful to fish and wildlife, and

commonly used in grazing management prescriptions. For example, field-based indicators of grazing pressure such as decreased stubble height, increased stream bank alteration, and decreased riparian vegetation cover have been linked to decreases in habitat quality for salmonid fishes [32, 34, 113, 114]. An important next step for monitoring with remote sensing is linking the response of conservation targets (i.e., rare taxa) or their specific habitat requirements to factors like NDVI, which can now be easily monitored using historical data archives and cloud computing.

Continued monitoring of our sites may reveal other restoration trajectories associated with grazing management and beaver as incised stream channels aggrade and fill behind beaver ponds [38], and help characterize the time required for additional recovery of riparian vegetation; low-gradient, larger streams in all study watersheds have inset channels below the historical floodplain and full recovery of potential vegetation at sites may require in excess of 5 decades [115]. For example, from 2016–2018 the Susie Creek pasture in Fig 4 has experienced beaver dam failure or abandonment as vegetation communities shifted from woody to emergent species (e.g., cattails, *Typha latifolia*), followed by early evidence of recolonization of willow within the elevated floodplain and the potential for a restart of the beaver colonization cycle. Long-term analyses of grazing treatments such as ours can be challenging due to the difficulty in tracking down historical records of grazing management, although recent efforts to document vegetation restoration treatments [116] and beaver-related restoration [117] do exist in the Great Basin.

Restoration with conservation grazing approaches and/or beaver management represents a low-effort and low-expense strategy for addressing causes of degradation using natural processes which can be scaled to broad spatial extents. Such strategies are increasingly valued relative to more traditional channel-based, active restoration approaches [118, 119]. As the result of those grazing management actions and compounded by the effect of natural beaver colonization, we demonstrate potential increases in riparian area productivity ranging up to 39% at sites with conservation-oriented grazing or exclosures and high beaver activity. These habitats represent an important mesic resource for fish and wildlife which is rare within the overall landscape, scarce on public lands in the ecoregion [18], and valued as a key resilient habitat in the face of changing climate [107–109].

Supporting information

S1 Dataset. Data used for analyses.
(XLSX)

S1 Fig. Predicted effect of beaver density on NDVI under three grazing treatments. Model selection results suggested that the most-plausible linear mixed model explaining variation in NDVI as a function of covariates included a grazing treatment x beaver density interaction term (Table 3). However, exploration of this top model revealed wide confidence intervals for the effect of beaver density under a conventional grazing regime. Further exploratory analysis of the data showed that beaver rarely occurred when under a Typical grazing regime, yielding much uncertainty in the parameter estimate and an unknown influence on model behavior. We therefore did not consider nor interpret models with the interaction term.
(TIF)

Acknowledgments

Jeffrey Moore provided grazing history information; Justin Huntington provided guidance on use of Google Earth Engine; Daniel McEvoy provided EDDI data for watersheds; Robin Bjork

and Sean McFall conducted preliminary identification of beaver dams; and Richard Lee georeferenced imagery. Helen Neville, Louisa Evers, Daniel McEvoy, and Michael Brown provided helpful review and comments on early versions of this manuscript.

Author Contributions

Conceptualization: Kurt A. Fesenmyer, Daniel C. Dauwalter, Carol Evans.

Data curation: Kurt A. Fesenmyer, Carol Evans, Todd Allai.

Formal analysis: Kurt A. Fesenmyer, Daniel C. Dauwalter.

Methodology: Kurt A. Fesenmyer, Daniel C. Dauwalter.

Validation: Carol Evans, Todd Allai.

Writing – original draft: Kurt A. Fesenmyer, Daniel C. Dauwalter.

Writing – review & editing: Carol Evans, Todd Allai.

References

1. Gregory SV, Swanson FJ, McKee WA, Cummins KW. An ecosystem perspective of riparian zones. BioScience. 1991 Sep 1; 41(8):540–51.
2. Naiman RJ, Decamps H, Pollock M. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications. 1993 May 1; 3(2):209–12. https://doi.org/10.2307/1941822 PMID: 27759328
3. Thomas JW, Maser C, Rodiek JE. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: riparian zones. Gen. Tech. Rep. PNW-GTR-080. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 1979; 80.
4. Knopf FL. Significance of riparian vegetation to breeding birds across an altitudinal cline. In Johnson RR, Zeibell CD, Patton DR, Ffolliott PF, Hamre RH (Tech. Coord.), Riparian Ecosystems and their Management: Reconciling Conflicting uses. First North American Riparian Conference, Rocky Mountain Forest and Range Experimental Station 1985 Apr 16. p. 105–111.
5. Smith GR, Dowling TE, Gobalet KW, Lugaski TS, Shiozawa DK, Evans RP. Biogeography and timing of evolutionary events among Great Basin fishes. Great Basin Aquatic Systems History. 2002; 33:175–234.
6. Sada DW, Vinyard GL. Anthropogenic changes in biogeography of Great Basin aquatic biota. Smithsonian Contributions to the Earth Sciences. 2002(33):277–94.
7. Crawford JA, Olson RA, West NE, Mosley JC, Schroeder MA, Whitson TD, et al. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management. 2004 Jan; 57(1):2–19.
8. Connelly JW, Rinkes ET, Braun CE. Characteristics of greater sage-grouse habitats: a landscape species at micro and macro scales. Studies in Avian Biology. 2011; 38:69–83.
9. Zoellick BW. Stream temperatures and the elevational distribution of redband trout in southwestern Idaho. The Great Basin Naturalist. 1999 Apr 1:136–43.
10. Dunham J, Schroeter R, Rieman B. Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. North American Journal of Fisheries Management. 2003 Aug 1; 23 (3):1042–9.
11. Dauwalter DC, Fesenmyer KA, Bjork R. Using aerial imagery to characterize redband trout habitat in a remote desert landscape. Transactions of the American Fisheries Society. 2015 Nov 1; 144(6):1322–39.
12. Zoellick BW, Cade BS. Evaluating redband trout habitat in sagebrush desert basins in southwestern Idaho. North American Journal of Fisheries Management. 2006 May 1; 26(2):268–81.
13. Brown DK, Echelle AA, Propst DL, Brooks JE, Fisher WL. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (Oncorhynchus gilae). Western North American Naturalist. 2001 Apr 1:139–48.
14. Dunham JB, Young MK, Gresswell RE, Rieman BE. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management. 2003 Jun 3; 178(1–2):183–96.

15. Brooks ML, Matchett JR, Shinneman DJ, Coates PS. Fire patterns in the range of the greater sage-grouse, 1984–2013—Implications for conservation and management. US Geological Survey; 2015. Open-File Report 2015–1167.
16. Schultz LD, Heck MP, Hockman-Wert D, Allai T, Wenger S, Cook NA, et al. Spatial and temporal variability in the effects of wildfire and drought on thermal habitat for a desert trout. Journal of Arid Environments. 2017 Oct 1; 145:60–8.
17. Matthews WJ, Marsh-Matthews E. Effects of drought on fish across axes of space, time and ecological complexity. Freshwater Biology. 2003 Jul 1; 48(7):1232–53.
18. Donnelly JP, Naugle DE, Hagen CA, Maestas JD. Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions. Ecosphere. 2016 Jan 1;7(1).
19. Stromberg JC, Lite SJ, Dixon MD. Effects of stream flow patterns on riparian vegetation of a semiarid river: implications for a changing climate. River Research and Applications. 2010 Jul; 26(6):712–29.
20. Kauffman JB, Krueger WC. Livestock impacts on riparian ecosystems and streamside management implications . . . a review. Journal of Range Management. 1984 Sep 1; 37(5):430–8.
21. Trimble SW, Mendel AC. The cow as a geomorphic agent A critical review. Geomorphology. 1995; 13:233–53.
22. Molles MC Jr, Dahm CN. A perspective on El Niño and La Niña: global implications for stream ecology. Journal of the North American Benthological Society. 1990 Mar 1; 9(1):68–76.
23. Holmgren M, Stapp P, Dickman CR, Gracia C, Graham S, Gutiérrez JR, et al. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environment. 2006 Mar 1; 4(2):87–95.
24. Westerling AL, Gershunov A, Brown TJ, Cayan DR, Dettinger MD. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society. 2003 May; 84(5):595–604.
25. Littell JS, McKenzie D, Peterson DL, Westerling AL. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecological Applications. 2009 Jun 1; 19(4):1003–21. PMID: 19544740
26. D'Antonio CM, Vitousek PM. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 1992 Nov; 23(1):63–87.
27. Balch JK, Bradley BA, D'antonio CM, Gómez-Dans J. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology. 2013 Jan 1; 19(1):173–83. https://doi.org/10.1111/gcb.12046 PMID: 23504729
28. Swanson SR, Wyman S, Evans C. Practical grazing management to meet riparian objectives. Journal of Rangeland Applications. 2015 Dec 23; 2:1–28.
29. Boyd CS, Beck JL, Tanaka JA. Livestock grazing and sage-grouse habitat: impacts and opportunities. Journal of Rangeland Applications. 2014 Mar 14; 1:58–77.
30. Arkle RS, Pilliod DS. Persistence at distributional edges: Columbia spotted frog habitat in the arid Great Basin, USA. Ecology and Evolution. 2015 Sep 1; 5(17):3704–24. https://doi.org/10.1002/ece3.1627 PMID: 26380699
31. Agouridis CT, Workman SR, Warner RC, Jennings GD. Livestock grazing management impacts on stream water quality: a review. JAWRA Journal of the American Water Resources Association. 2005 Jun 1; 41(3):591–606.
32. Saunders WC, Fausch KD. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. Transactions of the American Fisheries Society. 2007 Sep 1; 136(5):1216–30.
33. Walrath JD, Dauwalter DC, Reinke D. Influence of stream condition on habitat diversity and fish assemblages in an impaired upper Snake River Basin watershed. Transactions of the American Fisheries Society. 2016 Jul 1; 145(4):821–34.
34. Goss LM, Roper BB. The relationship between measures of annual livestock disturbance in western riparian areas and stream conditions important to trout, salmon, and char. Western North American Naturalist. 2018 Apr 30; 78(1):76–91.
35. Nussle S, Matthews KR, Carlson SM. Patterns and dynamics of vegetation recovery following grazing cessation in the California golden trout habitat. Ecosphere. 2017 Jul 1; 8(7).
36. Wyman S, Bailey D, Borman M, Cote S, Eisner J, Elmore W, et al. Riparian area management: grazing management processes and strategies for riparian-wetland areas. United States Department of the Interior, Bureau of Land Management, Technical Reference. 2006; 1737:1–05.
37. DeVries P, Fetherston KL, Vitale A, Madsen S. Emulating riverine landscape controls of beaver in stream restoration. Fisheries. 2012 Jun 1; 37(6):246–55.
38. Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C. Using beaver dams to restore incised stream ecosystems. Bioscience. 2014 Mar 24; 64(4):279–90.

39. Bouwes N, Weber N, Jordan CE, Saunders WC, Tattam IA, Volk C, et al. Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (Oncorhynchus mykiss). Scientific Reports. 2016 Jul 4; 6:28581. https://doi.org/10.1038/srep28581 PMID: 27373190

40. Hausner MB, Huntington JL, Nash C, Morton C, McEvoy DJ, Pilliod DS, et al. Assessing the effectiveness of riparian restoration projects using Landsat and precipitation data from the cloud-computing application ClimateEngine.org. Ecological Engineering. 2018 Sep 1; 120:432–40.

41. Gibson PP, Olden JD. Ecology, management, and conservation implications of North American beaver (Castor canadensis) in dryland streams. Aquatic Conservation: Marine and Freshwater Ecosystems. 2014 Jun 1; 24(3):391–409.

42. Pollock MM, Beechie TJ, Jordan CE. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. Earth Surface Processes and Landforms. 2007 Jul 1; 32(8):1174–85.

43. Demmer R, Beschta RL. Recent history (1988–2004) of beaver dams along Bridge Creek in central Oregon. Northwest Science. 2008 Sep; 82(4):309–18.

44. White SM, Rahel FJ. Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. Transactions of the American Fisheries Society. 2008 May 1; 137(3):881–94.

45. Weber N, Bouwes N, Pollock MM, Volk C, Wheaton JM, Wathen G, et al. Alteration of stream temperature by natural and artificial beaver dams. PLOS ONE. 2017 May 17; 12(5):e0176313. https://doi.org/10.1371/journal.pone.0176313 PMID: 28520714

46. Dauwalter DC, Walrath JD. Beaver dams, streamflow complexity, and the distribution of a rare minnow, Lepidomeda copei. Ecology of Freshwater Fish. 2018 Apr; 27(2):606–16.

47. Cooke HA, Zack S. Influence of beaver dam density on riparian areas and riparian birds in shrubsteppe of Wyoming. Western North American Naturalist. 2008 Sep; 68(3):365–73.

48. Huntington J, McGwire K, Morton C, Snyder K, Peterson S, Erickson T, et al. Assessing the role of climate and resource management on groundwater dependent ecosystem changes in arid environments with the Landsat archive. Remote Sensing of Environment. 2016 Nov 1; 185:186–97.

49. Huntington JL, Hegewisch KC, Daudert B, Morton CG, Abatzoglou JT, McEvoy DJ, et al. Climate Engine: cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bulletin of the American Meteorological Society. 2017 Nov; 98(11):2397–410.

50. Booth DT, Tueller PT. Rangeland monitoring using remote sensing. Arid Land Research and Management. 2003 Jan 1; 17(4):455–67.

51. Rouse J Jr, Haas RH, Schell JA, Deering DW. Monitoring vegetation systems in the Great Plains with ERTS. In: Proceedings of the Third Earth Resources Technology Satellite-1 Symposium; 1974. NASA, Greenbelt, MD, USA; 1974. p. 301–331.

52. Booth DT, Cox SE, Simonds G. Riparian monitoring using 2-cm GSD aerial photography. Ecological Indicators. 2007 Jul 1; 7(3):636–48.

53. Booth DT, Cox SE, Simonds G, Sant ED. Willow cover as a stream-recovery indicator under a conservation grazing plan. Ecological Indicators. 2012 Jul 1; 18:512–9.

54. Pearl CA, Adams MJ, Haggerty PK, Urban L. Using occupancy models to accommodate uncertainty in the interpretation of aerial photograph data: Status of beaver in Central Oregon, USA. Wildlife Society Bulletin. 2015 Jun 1; 39(2):319–25.

55. Omernik JM. Ecoregions of the conterminous United States. Annals of the Association of American Geographers. 1987 Mar 1; 77(1):118–25.

56. Poff N. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. Freshwater Biology. 1996 Aug; 36(1):71–9.

57. US Geological Survey. National Hydrography Geodatabase; 2013. Available: https://viewer.nationalmap.gov/viewer/nhd.html?p=nhd.

58. Gilbert JT, Macfarlane WW, Wheaton JM. The Valley Bottom Extraction Tool (V-BET): A GIS tool for delineating valley bottoms across entire drainage networks. Computers & Geosciences. 2016 Dec 1; 97:1–4.

59. US Geological Survey. National Elevation Dataset 1/3 arc-second; 2012. Available: https://nationalmap.gov/elevation.html.

60. Elko District Bureau of Land Management. Pasture Boundaries; 2013. [Dataset]

61. Oregon Bureau of Land Management. BLM OR Grazing Allotments and Pastures Polygon; 2010. Available: https://www.blm.gov/or/gis/data-details.php?id=31.

62. Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution. 2005 Sep 1; 20(9):503–10.

63. Bradley BA, O'sullivan MT. Assessing the short-term impacts of changing grazing regime at the landscape scale with remote sensing. International Journal of Remote Sensing. 2011 Oct 20; 32 (20):5797–813.

64. Sellers PJ. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing. 1985 Aug 1; 6(8):1335–72.

65. US Geological Survey. Landsat Collection 1 Level 1 Product Definition, version 1.0; 2017. Available: https://landsat.usgs.gov/sites/default/files/documents/LSDS-1656_Landsat_Level-1_Product_Collection_Definition.pdf.

66. Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment. 2017 Dec 1; 202:18–27.

67. Bradley BA, Mustard JF. Comparison of phenology trends by land cover class: a case study in the Great Basin, USA. Global Change Biology. 2008 Feb 1; 14(2):334–46.

68. Roy DP, Kovalskyy V, Zhang HK, Vermote EF, Yan L, Kumar SS, Egorov A. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. Remote Sensing of Environment. 2016 Nov 1; 185:57–70.

69. Eidenshink J, Schwind B, Brewer K, Zhu Z, Quayle B, Howard S. A project for monitoring trends in burn severity. Fire Ecology Special Issue. 2007; 3(1):3–21.

70. Thornton PE, Thornton MM, Mayer BW, Wilhelmi N, Wei Y, Cook RB. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2; 2012 Available: http://daac.ornl.gov.

71. National Ocean and Atmospheric Adminstration Earth System Research Labortory. EDDI Map Archive; 2017. Available: https://www.esrl.noaa.gov/psd/eddi.

72. US Environmental Protection Agency and US Geological Survey. National Hydrography Database–Plus, version 2; 2012. Available: http://www.horizon-systems.com/NHDPlus/NHDPlusV2_data.php.

73. Sarr DA. Riparian livestock exclosure research in the western United States: a critique and some recommendations. Environmental Management. 2002 Oct 1; 30(4):516–26. PMID: 12481918

74. Holbert MR. Whitehorse Butte allotment—controversy to compromise. Rangelands. 1991 Jun 1; 13 (3):125–8.

75. Dufurrena C. Rough and beautiful places. Range Magazine. Jun 2016. Available from: http://www.rangemagazine.com/features/summer-16/range-su16-rough-and-beautiful.pdf.

76. McAdoo K, Peterson C, Boies R, Smith A, Moore J, Coffin P. Shoesole Resource Managment Group Case Study: 20 Years of Collaborative Conservation Success. University of Nevada Cooperative Extension; 2017.

77. Baker BW, Ducharme HC, Mitchell D, Stanley TR, Peinetti HR. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications. 2005 Feb 1; 15(1):110–8.

78. Dwire KA, Kauffman JB. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management. 2003 Jun 3; 178(1–2):61–74.

79. Patten DT. Riparian ecosytems of semi-arid North America: Diversity and human impacts. Wetlands. 1998 Dec 1; 18(4):498–512.

80. Bendix J, Hupp CR. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes. 2000 Nov; 14(16-17):2977–90.

81. Stromberg JC, Beauchamp VB, Dixon MD, Lite SJ, Paradzick C. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. Freshwater Biology. 2007 Apr; 52(4):651–79.

82. Boudell JA, Dixon MD, Rood SB, Stromberg JC. Restoring functional riparian ecosystems: concepts and applications. Ecohydrology. 2015 Jul; 8(5):747–52.

83. Hobbins MT, Wood A, McEvoy DJ, Huntington JL, Morton C, Anderson M, Hain C. The evaporative demand drought index. Part I: Linking drought evolution to variations in evaporative demand. Journal of Hydrometeorology. 2016 Jun; 17(6):1745–61.

84. McEvoy DJ, Huntington JL, Hobbins MT, Wood A, Morton C, Anderson M, Hain C. The evaporative demand drought index. Part II: CONUS-wide assessment against common drought indicators. Journal of Hydrometeorology. 2016 Jun; 17(6):1763–79.

85. Carlisle DM, Falcone J, Wolock DM, Meador MR, Norris RH. Predicting the natural flow regime: models for assessing hydrological alteration in streams. River Research and Applications. 2010 Feb; 26 (2):118–36.

86. Church M. Geomorphic thresholds in riverine landscapes. Freshwater Biology. 2002 Apr; 47(4):541–57.

87. Macfarlane WW, Wheaton JM, Bouwes N, Jensen ML, Gilbert JT, Hough-Snee N, et al. Modeling the capacity of riverscapes to support beaver dams. Geomorphology. 2017 Jan 15; 277:72–99.

88. Small BA, Frey JK, Gard CC. Livestock grazing limits beaver restoration in northern New Mexico. Restoration Ecology. 2016 Sep 1; 24(5):646–55.

89. Burnham KP, Anderson DR. Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer Science & Business Media; 2003.

90. Nakagawa S, Schielzeth H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution. 2013 Feb 1; 4(2):133–42.

91. Shipley B. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R. Cambridge: Cambridge University Press; 2000.

92. Grace JB, Pugesek BH. On the use of path analysis and related procedures for the investigation of ecological problems. The American Naturalist. 1998 Jul; 152(1):151–9. https://doi.org/10.1086/286156 PMID: 18811408

93. Rosseel Y. Lavaan: An R package for structural equation modeling and more. Journal of Statistical Software. 2012 Sep 12; 48(2):1–36.

94. Epskamp S. semPlot: Unified visualizations of structural equation models. Structural Equation Modeling: A Multidisciplinary Journal. 2015 Jul 3; 22(3):474–83.

95. Arnold TW. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management. 2010 Aug; 74(6):1175–8.

96. Holland KA, Leininger WC, Trlica MJ. Grazing history affects willow communities in a montane riparian ecosystem. Rangeland Ecology & Management. 2005 Mar; 58(2):148–54.

97. Dalldorf KN, Swanson SR, Kozlowski DF, Schmidt KM, Shane RS, Fernandez G. Influence of livestock grazing strategies on riparian response to wildfire in northern Nevada. Rangeland Ecology & Management. 2013 Jan; 66(1):34–42.

98. Hough-Snee N, Roper BB, Wheaton JM, Budy P, Lokteff RL. Riparian vegetation communities change rapidly following passive restoration at a northern Utah stream. Ecological Engineering. 2013 Sep 1; 58:371–7.

99. Batchelor JL, Ripple WJ, Wilson TM, Painter LE. Restoration of riparian areas following the removal of cattle in the Northwestern Great Basin. Environmental Management. 2015 Apr 1; 55(4):930–42. https://doi.org/10.1007/s00267-014-0436-2 PMID: 25694035

100. Dauwalter DC, Fesenmyer KA, Miller SW, Porter T. Response of Riparian Vegetation, Instream Habitat, and Aquatic Biota to Riparian Grazing Exclosures. North American Journal of Fisheries Management. 2018 Oct 1; 38(5):1187–200.

101. Silverman NL, Allred BW, Donnelly JP, Chapman TB, Maestas JD, Wheaton JM, et al. Low-tech riparian and wet meadow restoration increases vegetation productivity and resilience across semiarid rangelands. Restoration Ecology. 2018.

102. Baker BW, Peinetti HR, Coughenour MB, Johnson TL. Competition favors elk over beaver in a riparian willow ecosystem. Ecosphere. 2012 Nov 1; 3(11):1–5.

103. Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. Rapid range shifts of species associated with high levels of climate warming. Science. 2011 Aug 19; 333(6045):1024–6. https://doi.org/10.1126/science.1206432 PMID: 21852500

104. McCain CM, Colwell RK. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecology Letters. 2011 Dec 1; 14(12):1236–45. https://doi.org/10.1111/j.1461-0248.2011.01695.x PMID: 21981631

105. Isaak DJ, Young MK, Nagel DE, Horan DL, Groce MC. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology. 2015 Jul 1; 21(7):2540–53. https://doi.org/10.1111/gcb.12879 PMID: 25728937

106. Dai A. Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change. 2011 Jan 1; 2(1):45–65.

107. Seavy NE, Gardali T, Golet GH, Griggs FT, Howell CA, Kelsey R, et al. Why climate change makes riparian restoration more important than ever: recommendations for practice and research. Ecological Restoration. 2009 Sep 1; 27(3):330–8.

108. Capon SJ, Chambers LE, Mac Nally R, Naiman RJ, Davies P, Marshall N, et al. Riparian ecosystems in the 21st century: hotspots for climate change adaptation? Ecosystems. 2013 Apr 1; 16(3):359–81.

109. Timpane-Padgham BL, Beechie T, Klinger T. A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. PLOS ONE. 2017 Mar 16; 12(3):e0173812. https://doi.org/10.1371/journal.pone.0173812 PMID: 28301560

110. Holmgren M, Scheffer M. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems. 2001 Mar 1; 4(2):151–9.

111. Shafroth PB, Stromberg JC, Patten DT. Riparian vegetation response to altered disturbance and stress regimes. Ecological Applications. 2002 Feb 1; 12(1):107–23.

112. Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, Riper CV, Weeks EP, Stuart JN. Control of Tamarix in the western United States: implications for water salvage, wildlife use, and riparian restoration. Environmental Management. 2005 Mar 1; 35(3):231–46. https://doi.org/10.1007/s00267-004-0099-5 PMID: 15925969

113. Li HW, Lamberti GA, Pearsons TN, Tait CK, Li JL, Buckhouse JC. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society. 1994 Jul 1; 123(4):627–40.

114. Zoellick BW. Density and biomass of redband trout relative to stream shading and temperature in southwestern Idaho. Western North American Naturalist. 2004 Feb 1:18–26.

115. Beechie TJ, Pollock MM, Baker S. Channel incision, evolution and potential recovery in the Walla Walla and Tucannon River basins, northwestern USA. Earth Surface Processes and Landforms. 2008 Apr 30; 33(5):784–800.

116. Pilliod DS, Welty JL, Toevs GR. Seventy-five years of vegetation treatments on public rangelands in the great basin of North America. Rangelands. 2017 Feb; 39(1):1–9.

117. Pilliod DS, Rohde AT, Charnley S, Davee RR, Dunham JB, Gosnell H, et al. Survey of beaver-related restoration practices in rangeland streams of the western USA. Environmental Management. 2018 Jan 1; 61(1):58–68. https://doi.org/10.1007/s00267-017-0957-6 PMID: 29167949

118. Beechie TJ, Sear DA, Olden JD, Pess GR, Buffington JM, Moir H, et al. Process-based principles for restoring river ecosystems. BioScience. 2010 Mar 1; 60(3):209–22.

119. Bernhardt ES, Palmer MA. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. Ecological Applications. 2011 Sep; 21(6):1926–31. PMID: 21939034



Greater Sage-Grouse in the Southeast Montana Sage-Grouse Core Area

MONTANA FISH, WILDLIFE AND PARKS (FWP)
in partnership with:
USDI BUREAU OF LAND MANAGEMENT (BLM)

Melissa A. Foster[1], John T. Ensign[2], Windy N. Davis[3], and Dale C. Tribby[4]

1: FWP Wildlife Biologist. Phone: (406) 852-2032. Email: mfoster@mt.gov.
2: FWP Wildlife Program Manager. Phone: (406) 234-0921. Email: jensign@mt.gov.
3: Former FWP Energy Specialist & BLM Liaison. Phone: (208) 756-2271. Email: windy.davis@idfg.idaho.gov.
4: BLM Supervisory Wildlife Biologist. Phone: (406) 233-2812. Email: dtribby@blm.gov.



– EXECUTIVE SUMMARY –

We studied 94 greater sage-grouse hens in the Southeastern Montana Sage-Grouse Core Area (hereafter: Core Area) to determine demographic rates, quantify seasonal movements and habitat use, and make management recommendations. Sage-grouse Core Areas support Montana's highest densities of sage-grouse, and are high priority conservation focus areas critical to the long term sustainability and management of sage-grouse. Historic lek data (pre-1980) from the Core Area are unavailable, but lek counts conducted over the past 30 years indicate the population has not exhibited a long-term downward trend. The population peaked during the mid-2000's but declined following a West Nile virus (WNv) outbreak in 2007. Sage-grouse have persisted at sustainable levels in the Core Area because traditional landowners have maintained large expanses of intact sagebrush-steppe habitat.

Sage-grouse in southeastern Montana were exposed to extreme weather conditions throughout the study. Precipitation during spring/summer 2010 was 53% above average. Precipitation during spring/summer 2011 was 67% above average, with 8 inches rainfall during May alone, which caused widespread flooding (100-year flood events). Drought conditions occurred during summer 2012. Above-average snowfall and below-average temperatures occurred during winter 2009-10. The following winter, 2010–11, was among the most severe on record (30 year winter event). In contrast, winter 2011–12 was among the mildest on record.

Nest initiation (91%) and renest initiation (42%) rates were high. Apparent nest success varied among years (43% in 2010, 33% in 2011, and 68% in 2012). Low nest success in 2011 was driven by extreme precipitation that caused 9% of nests to fail and depressed hatch rates. Models relating vegetation characteristics to nest survival generally performed poorly, which indicates cover did not limit nest success during the study. Chick survival averaged 29%. Forb cover was higher for successful (12.2% cover) than failed (7.9% cover) broods. Forb cover and richness were related to precipitation and higher during wet years.

Apparent nest success was higher for nests in pastures with livestock concurrently present (59%) than pastures without livestock (38%), and we observed no direct negative impacts (e.g., trampling) of livestock on nesting sage-grouse. Similarly, brood success from 0–14 days post-hatch was higher for broods hatched in pastures with livestock (79%) than without (61%). The mechanism driving this is unknown; it may have resulted from behavioral avoidance of livestock by predators, or reflect predator control efforts in areas with livestock. Our results concur with research elsewhere that livestock grazing is compatible with sage-grouse conservation.

During wet years 2010 and 2011, 36% of hatches and the bulk of the early brood-rearing period occurred after June 15 (a common end date for timing restrictions on disturbing activities associated with development projects). During drought year 2012, all nests hatched by June 10 but the early brood-rearing period extended to mid-July. We recommend timing restrictions be maintained until July 15: in most years nesting would be complete, nearly all chicks would be >2 weeks old, and most broods would have reached 30 days. Extending timing restrictions to benefit young chicks may be important because most chick mortality occurs

within the first 4 weeks post-hatch, and chick survival is one of the most important parameters influencing population growth for sage-grouse. However, timing restrictions are only effective for minimally invasive, short duration projects and cannot offset the impacts of long-term habitat loss, fragmentation, or degradation.

The average distance between nests and the nearest lek was 1.15 miles, which may reflect low levels of fragmentation and relatively intact sagebrush-steppe habitat in the Core Area. Fifty-nine percent of nests were within one mile of a known lek location, 84% within 2 miles, 93% within 3 miles, and 97% within 4 miles. Nest success exerts great influence on population growth rates for sage-grouse. Therefore, a one-mile buffer is inadequate to avoid significant population impacts associated with development activities. We recommend a minimum 4 mile buffer around leks for highly-intrusive practices within suitable sagebrush habitat. A 4 mile buffer may not be feasible in all cases. As with any project or planned development, consultation with an area wildlife biologist, early in the process, is critical to avoid or minimize impacts. Brood hens tended to stay close to nest sites for the first 30 days following hatch ($\bar{x}$ = 0.68 mi), thus restrictive radii placed around leks may also benefit young broods.

Annual hen survival in the Core Area during 2011–12 and 2012–13 (59–61%) was higher than survival during 2010–11 (45%), which was driven by lower late summer/fall survival (due to a suspected WNv outbreak) and lower winter survival due to severe conditions. Mortality was attributed to primarily avian (≥40%) followed by mammalian predation (≥27%). No mortalities were attributed to collision with fences or power lines, and no hunting mortalities occurred. Population Viability Analyses (PVA) indicated that Core Area sage-grouse are very likely to persist at sustainable levels. Our most realistic scenario suggested a stable population (population growth rate = -0.8% annually) and 0% probability of extinction within 30 years. Severe weather events (floods and winter) had little impact on population growth (≤ 0.4% reduction in annual population growth) because of their rarity. The future impact of WNv is of concern because few tools exist to reduce WNv outbreaks, the severity of future outbreaks is impossible to reliably predict, and PVA indicated that the Core Area sage-grouse population is not undergoing rapid recovery since the 2007 outbreak. However, PVA did indicate the population has great potential to increase if environmental conditions or management actions improve population vital rates (e.g., 17.5% increase in annual population growth rate by increasing survival and reproduction rates by 5%).

We designated 19% of the Core Area as sage-grouse winter range. Critical winter range consisted of windswept flats characterized by short shrubs ($\bar{x}$ = 7.8 in), and moderate shrub density ($\bar{x}$ = 11%). Hens used areas with taller ($\bar{x}$ = 10.2 in) sagebrush during severe winter 2010–11, and 54% percent of hens shifted their winter ranges, presumably to locate open stands of sagebrush. Other hens were apparently unable to locate suitable habitat, based on reduced survival and observations of sage-grouse roosting on a barren snowscape during the severe winter. Sage-grouse winter habitat use reflects that the Core Area is located at the eastern edge of the range of Wyoming big sagebrush, and is characterized by smaller, less dense sagebrush than elsewhere in the sage-grouse range. Sage-grouse in the study used sagebrush-steppe habitat extensively throughout their annual cycle (92% of locations), but frequently (27% of locations) used areas with sparse (1–10%) sagebrush canopy cover. Given

that sagebrush characteristics may be intrinsically limited by local soil and climactic conditions, management guidelines that emphasize certain heights or densities of sagebrush may be unachievable in the Core Area. Management of sage-grouse habitat should focus on protecting the integrity of winter use and other important areas rather than sagebrush manipulation.

Movement patterns varied greatly among individual sage-grouse hens but the Core Area boundary in Montana contained nearly every location in the state, which provides evidence that the core area approach (i.e., delineating priority areas for sage-grouse conservation based on lek densities) has great potential to benefit sage-grouse. However, many hens made movements into South Dakota and Wyoming adjacent to the Core Area, and cooperation among states will be necessary to maintain this sage-grouse population. We recommend minor adjustments to the Montana Core Area and Wyoming Connectivity area to create a cohesive boundary and incorporate winter range. The South Dakota draft core area encompassed nearly all locations from radio-collared sage-grouse hens.

Traditional family-owned ranching operations, the predominant local stakeholders in the Core Area, have historically managed land in a manner that is compatible with sage-grouse conservation and are well-poised to collaborate with wildlife and range professionals to maintain and improve sage-grouse habitat. Our management recommendations are standard for sage-grouse and include the following: 1) first and foremost, maintain large expanses of intact sagebrush habitat, 2) utilize livestock grazing as a management tool (we recommend rotational grazing systems consisting of large pastures that incorporate rest during the growing season and alternate season of use), 3) implement conservation efforts on a landscape scale, including various stakeholders, 4) when projects must occur, plan to minimize the impacts, and 5) minimize the potential for WNv outbreaks where possible. We do not recommend predator control for several reasons: 1) population vital rates observed in the study were normal for sage-grouse and we expected the majority of mortalities and nest failures to be a result of predation (sage-grouse are a prey species—they do not typically die of old age, and nest predation is a fact of life that all ground nesting birds have evolved with), 2) controlling avian predators is not possible due to federal law (e.g., 1940 Bald and Golden Eagle Protection Act), 3) control of one type of predator often leads to unintended increases in other predator species, 4) predator control is expensive and only effective in the short term in small areas with intense control of all predators. In contrast, habitat management can result in economically feasible, widespread, long-term benefits for sage-grouse and livestock producers alike.

– TABLE OF CONTENTS –

Executive Summary ..... **i**

List of Tables ..... **vi**

List of Figures ..... **viii**

1. Introduction **1**
Study Area 5
Capture & Radiotelemetry 6

2. Nest Success & Vegetation **9**
Introduction 10
Methods 11
Nest monitoring 11
Vegetation sampling 11
Analyses 12
Results 13
Nesting season dates 13
Nesting vital rates 14
Fates of failed nests 15
Nest vegetation 16
Factors influencing nest survival 18
Discussion 20

3. Brood Success & Vegetation **25**
Introduction 26
Methods 27
Brood monitoring 27
Brood site vegetation 28
Analyses 28
Results 29
Brood-rearing dates & vital rates 29
Brood site vegetation 31
Factors influencing brood survival 33
Discussion 37

4. Hen Survival **42**
Introduction 43
Methods 43
Results 44
Discussion 46

5. Population Viability **48**
Introduction 49

Methods 50
Scenarios 51
Results 53
Discussion 53

6. Movements & Seasonal Habitat Use 56
Introduction 57
Methods 57
Analyses 58
Results 60
Movements 60
Seasonal habitat use 62
Discussion 67

7. Winter Use & Vegetation 72
Introduction 73
Methods 73
Delineating winter use areas 73
Winter vegetation 74
Results 75
Delineating winter use areas 75
Winter vegetation 76
Discussion 79

8. Management Recommendations 82
Maintain Large Expanses of Intact Sagebrush Habitat 83
Management of sagebrush habitat 84
Utilize Livestock Grazing as a Management Tool 85
Predator Control vs. Habitat Management 87
Implement Conservation Efforts on a Landscape Scale 88
When Projects Must Occur, Plan to Minimize the Impacts 89
Breeding, nesting, and brood-rearing 90
Winter Range 91
Minimize West Nile Virus Outbreaks 91

Acknowledgements 93

Literature Cited 94

Appendix A: Weather Conditions 105

– LIST OF TABLES –

Table 2.1. Median incubation initiation date and nesting season length 14

Table 2.2. Nest and renest initiation by age class and year 14

Table 2.3. Apparent nest success and maximum-likelihood estimates for nest success 15

Table 2.4. Vegetation characteristics at sage-grouse nest sites 17

Table 2.5. Ranking of model strengths for daily survival rates (DSR) of sage-grouse-nests 19

Table 3.1. Median and range of hatch dates 30

Table 3.2. Brood success 31

Table 3.3. Average number of chicks per successful brood at 30 days post-hatch, chick survival, and chick production per hen 31

Table 3.4. Shrub characteristics at sage-grouse brood-rearing locations 32

Table 3.5. Vegetative characteristics at sage-grouse brood-rearing locations 32

Table 3.6. Forb species richness at sage-grouse brood rearing locations 33

Table 3.7. Percent occurrence of 7 common forb species at sage-grouse brood-rearing locations and average percent horizontal cover of each species 34

Table 3.8. Percent occurrence for forb species occurring at <15% of brood-rearing locations 35

Table 4.1. Ranking of model strengths for hen survival 44

Table 4.2. Seasonal and annual survival 45

Table 5.1. Parameter estimates for population viability analysis scenarios. 52

Table 5.2. Population viability analysis results 53

Table 6.1. Distances between nests for hens that nested more than once during the study 61

Table 6.2. Distances between nest and brooding sites 61

Table 6.3. Average distance and total distance moved over winter 67

Table 6.4. Fidelity to winter range for hens that were tracked more than one winter 67

Table 6.5. Habitat use by season and reproductive status 68

Table 7.1. Sagebrush canopy cover, density, and height at sage-grouse winter locations..... 77

Table 7.2. Slope was lower in critical versus important sage-grouse winter range 78

Table 7.3. Percent of sage-grouse winter locations that were within 0.25 miles from fences, roads, trees, power lines, buildings, structures, or trees 78

Table A.1. Spring/summer monthly precipitation totals 105

Table A.2. Spring/summer monthly average temperatures 106

Table A.3. Total monthly snowfall 107

Table A.4. Winter monthly average temperatures 108

– LIST OF FIGURES –

Fig. 1.1. Current and historic distribution of greater sage-grouse 2

Fig. 1.2. Sage-grouse Core Areas and study area..... 4

Fig. 1.3. Average number of greater sage-grouse males counted per lek in Carter County, Montana, 1980-2013 5

Fig. 1.4. The Southeast Montana Sage-grouse Core Area contains large tracts of sagebrush-steppe habitat. 6

Fig. 1.5. Capture locations for 94 radio collared sage-grouse hens 7

Fig. 2.1. Nearly all nest failures were a result of depredation. However, a 100-year flood event in 2011 caused 9% of nests to fail and reduced the hatch rate for many nests when one or more eggs were partially buried in mud, making it impossible for the egg to maintain adequate temperature for development 16

Fig. 2.2. Percent horizontal cover of 5 cover classes estimated within Daubenmire (1959) frames along transects bisecting sage-grouse nests 18

Fig. 2.3. Results from other studies indicate that sage-grouse nests tend to be more successful when surrounding grass is taller 22

Fig. 3.1. Two week old chicks were often fully concealed underneath brood hens at night. As chicks approach 30 days old, they are too large to be fully concealed beneath the hen and can be accurately counted during nighttime brood counts 27

Fig. 3.2. Range of hatch dates, median hatch date, and early brood rearing period..... 30

Fig. 3.3. Average percent horizontal cover for 5 habitat variables measured within Daubenmire (1959) frames along transects at sage-grouse brood-rearing locations, 2010–2012 32

Fig. 3.4. Example brood rearing locations for radio collared greater sage-grouse 36

Fig. 3.5. Sweet clover dominated much of the landscape of the study area during 2011..... 41

Fig. 4.1. Cause-specific mortality 45

Fig. 4.2. Heavy snow cover during winter 2010–2011 reduced hiding cover and concentrated sage-grouse..... 47

Fig. 5.1. Example VORTEX simulation 49

Fig. 6.1. Example movement patterns..... 63

Fig. 6.2. Example minimum convex polygons..... 64

Fig. 6.3. Overall dispersion of radio-collared sage-grouse during the breeding, nesting/brood-rearing, and late summer/fall seasons. 65

Fig. 6.4. Overall dispersion of radio-collared sage-grouse during winter 66

Fig. 7.1. Winter range polygons 76

Fig. 7.2. Examples of shrub characteristics at winter locations 77

Fig. 7.3. Rose diagram showing aspects for winter locations. 78

Fig. 7.4. Winter use data was scarce for hens from the extreme northeast finger of the Core Area due to hen mortalities. It is likely that other, unidentified, winter use areas exist in Core Area south of Powderville, MT 80

Fig. A.1. Extraordinary precipitation during spring/summer 2010 and 2011 resulted in tremendous growth of vegetation during both years 106

Fig. A.2. The Little Missouri River north of Albion, MT rose above 100-year flood levels during spring 2011 106

Fig. A.3. Below-average precipitation and above-average temperatures resulted in drought conditions during summer 2012 107

Fig. A.4. Snowfall during winter 2010-11 was nearly three times average, resulting in a vast snowscape and deep snow drifts throughout the Core Area 108

Fig. A.5. Above-average temperatures and below-average snowfall during winter 2011-12 resulted in mild, open conditions 108



Photo Courtesy of Chad Cyrus

– 1 –

Introduction







Greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) have been reduced to less than 60% of their historic range (Schroeder et al. 2004; Fig. 1.1), and calls for their protection began nearly 100 years ago (Hornaday 1916). Habitat loss, fragmentation (e.g., from tillage agriculture, sub-division, or energy development), and degradation (e.g., due to fire or herbicide application) are the primary mechanisms that resulted in sage-grouse declines (Connelly et al. 2011*b,* Knick and Connelly 2011). More recently, West Nile Virus (WNv) has resulted in rapid, significant reductions in local sage-grouse populations range-wide (Naugle et al. 2005, USFWS 2010). In response to population declines, a number of petitions to list the species under the Endangered Species Act (ESA) were initiated, beginning in 1999. In February 2010, the United States Fish and Wildlife Service (USFWS) determined that ESA listing of sage-grouse was warranted but precluded due to the number of other species at more imminent risk of extinction, and sage-grouse were listed as a "candidate" species (USFWS 2010). The candidate status does not provide sage-grouse protection under ESA, but does require the

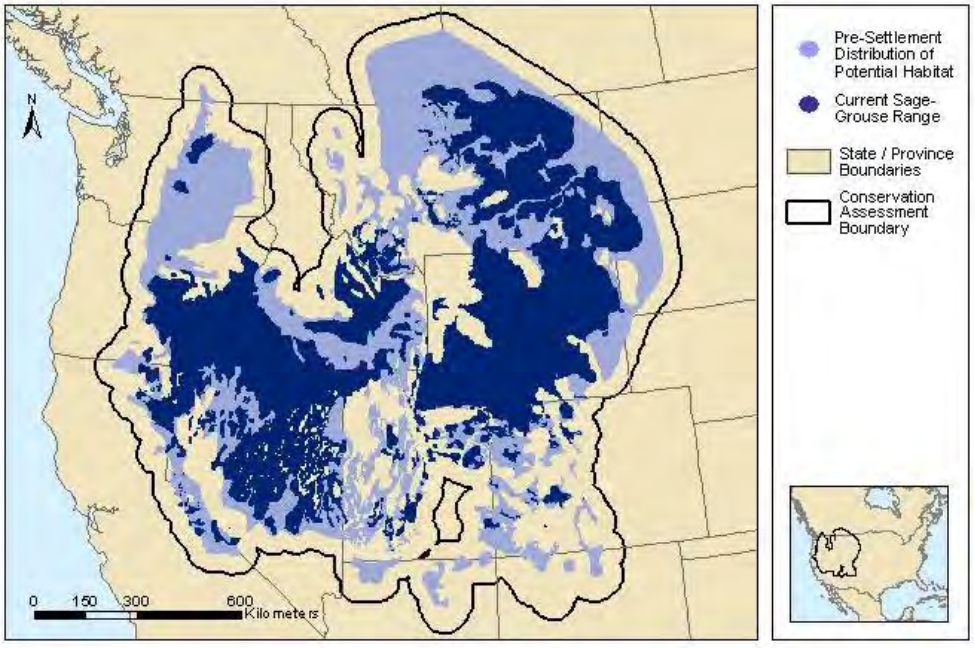


Figure 1.1. Current and historic distribution of greater sage-grouse. The current distribution was based on survey (lek, brood, winter), harvest, and radiotelemetry data. The historic distribution was based on the historic distribution of suitable sagebrush habitat and was verified using museum specimens and historic observations of sage-grouse from the early 1800's and later. Figure source: Knick and Connelly (2011) based on data compiled by Schroeder et al. (2004).

USFWS to annually review their status. This elevated status also brings about a sense of urgency to prevent ESA listing through conservation measures such as habitat protection and enhancement.

Despite population declines throughout much of the sage-grouse range, portions of southeast Montana support stable sage-grouse populations and contain large areas of unfragmented sagebrush-steppe habitat (Taylor et al. 2010). Montana Fish, Wildlife, and Parks (FWP) historically monitored sage-grouse populations using hunter harvest surveys, lek counts in a small number of geographically defined trend areas, and other opportunistic lek counts (typically large, easily accessible leks). In response to increasing concerns over sage-grouse populations elsewhere and lack of comprehensive lek documentation, FWP Region 7 initiated systematic aerial survey efforts across all potential sage-grouse habitat in the region to identify previously unknown lek locations and quantify male lek attendance. The surveys occurred over a 10-year period and nearly doubled the number of documented lek locations in southeastern Montana (Beyer et al. 2010). For example, of the 234 leks currently documented in Carter and Powder River Counties, 93 (40%) were identified during systematic aerial surveys between 2006 and 2009.

In 2009, FWP used lek location and male attendance data to delineate Sage-grouse Core Areas (Fig. 1.2). Sage-grouse Core Areas support Montana's highest densities of sage-grouse, and are high priority conservation focus areas deemed critical to the long term sustainability and management of sage-grouse. The Sage-grouse Core Area in the southeastern corner of Montana (Fig. 1.2; hereafter: Core Area) is of particular interest because it remains largely intact (Taylor et al. 2010) and it may provide connectivity among sage-grouse populations in Wyoming, South Dakota, and elsewhere in Montana. Lek counts have been conducted in the southeasternmost core area since the 1980's primarily by FWP and BLM biologists, and the American Colloid Company has surveyed leks adjacent to their active bentonite mines since 1993. Lek survey efforts have increased through time, concurrent with concerns about sage-grouse conservation. The average number of males per lek in Carter County peaked during the mid-2000's, but declined following a WNv outbreak during 2007 (Fig. 1.3; Centers for Disease Control 2013). Although the average number of males per lek has varied annually during the

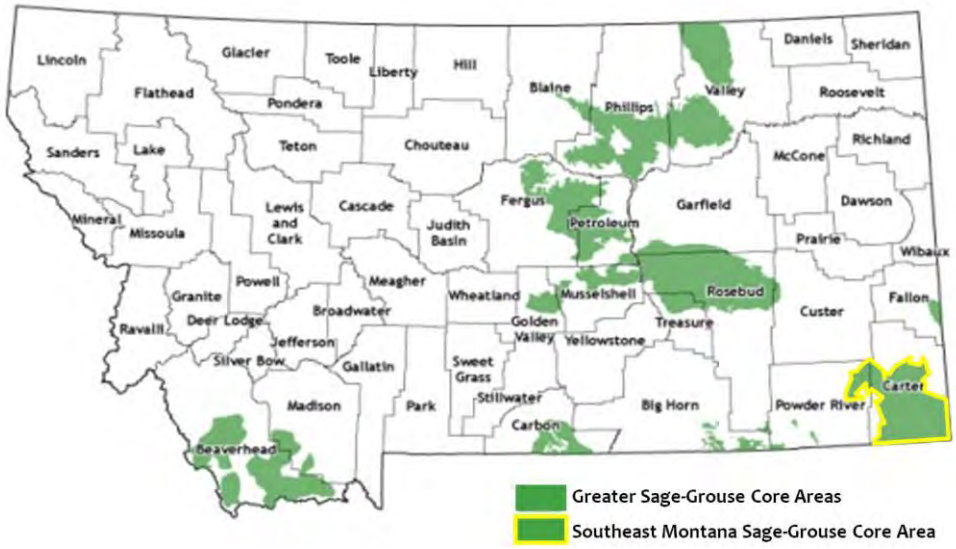


Figure 1.2. Sage-grouse Core Areas (green) support Montana's highest densities of Greater Sage-Grouse (upper 25% quartile), and are deemed vitally important to the long term conservation, sustainability and management of sage-grouse. Research efforts were focused in the Southeast Montana Sage-Grouse Core Area (yellow outline) in Carter and Powder River Counties, Montana.

last 3 decades, the population does not exhibit a long-term downward trend characteristic of imperiled sage-grouse populations elsewhere. However, the status of Core Area sage-grouse relative to historic numbers is unknown because lek data are not available prior to 1980.

Aerial surveys have provided a wealth of information about important sage-grouse breeding areas in the Core Area, but very little was known about other critical periods (e.g., nesting, brood-rearing, winter), movements, habitat use, or population vital rates. Therefore, our objectives were to: 1) determine demographic rates (i.e., nest success, brood success, hen survival), and identify sources of hen mortality (e.g., predation, WNv, hunting); 2) identify seasonal movements and migration patterns, and assess the adequacy of the size of the Core Area to accommodate the life history needs of the sage-grouse population; 3) identify seasonal habitat use, relate vegetation structure to nest success, and quantify habitat conditions under current land management, and 4) identify potential limiting factors for sage-grouse populations in the Core Area and recommend management strategies and mitigation measures. Results from this project will aid in land use planning, prioritization of conservation and restoration efforts, and provide information to assess the effects of future land use changes.

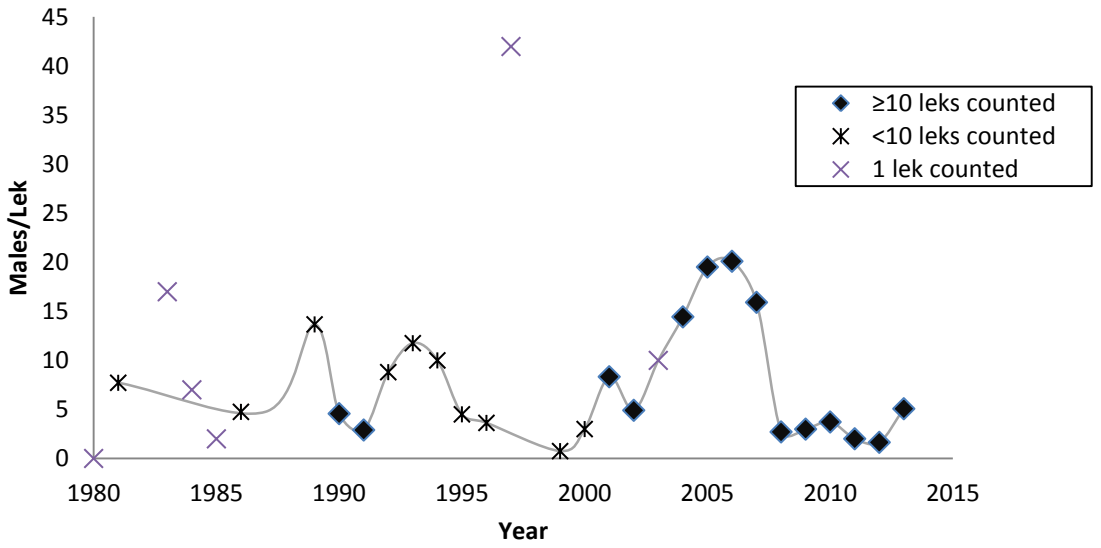


Figure 1.3. Average number of greater sage-grouse males counted per lek in Carter County, Montana, 1980–2013. Lek survey effort differed among years, with 0–107 leks surveyed in a single year. Lek counts peaked during springs 2004–2007, but fell following a significant West Nile virus outbreak in Montana during late summer 2007 (Centers for Disease Control 2013).

Study area

The Core Area is located in Carter and Powder River counties (Fig. 1.2). It extends east from the Powder River to the South Dakota border, and south from the Powderville Road to the Wyoming border. The area is dominated by sagebrush-steppe vegetation with interspersed native and introduced grasslands. The dominant shrub is Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) followed by plains silver sage (*A. cana* ssp. *cana*) and greasewood (*Sarcobatus vermiculatus*). Livestock grazing is the dominant land use. Negligible levels of tillage have occurred within the Core Area (Taylor et al. 2010), although some areas have been converted to hay and small grain production. Bentonite surface mining and limited natural gas extraction occur in the southern portion of the Core Area, and several buried oil and gas transmission pipelines traverse the Core Area. There is potential for future expansion of bentonite mining, oil and gas development, and wind energy development within the Core Area, along with continued construction of oil and gas transmission pipelines. The Core Area is a mix of private (54%), federal (BLM; 36%) and state (Montana Department of Natural Resources and Conservation; 10%) surface ownership (NRCS 2010).



Figure 1.4. The Southeast Montana Sage-grouse Core Area contains large expanses of intact sagebrush-steppe habitat.

Capture & radiotelemetry

We captured a total of 94 sage-grouse hens between spring 2009 and spring 2012 (2009 = 12, 2010 = 54, 2011 = 27, 2012 = 1; Fig. 1.5). All hens were captured using the nighttime spotlighting and hoop-netting technique (Wakkinen et al. 1992). We used plumage characteristics to determine age for each hen (yearling or adult; Eng 1955, Crunden 1963), and

fitted each with an individually numbered aluminum leg band (National Band and Tag Company, Newport, Kentucky) and a necklace-type radio transmitter (Advanced Telemetry Systems®, Isanti, Minnesota). Transmitters weighed <2% of a hen's body weight.

For spring captures, we used data from concurrent aerial and ground lek surveys to inform capture efforts, and focused our capture efforts surrounding leks where males were observed. We attempted to avoid "big lek bias" (i.e., preferentially capturing hens from large leks) by limiting the number of hens captured per lek ($\bar{x}$ = 2.7 hens/lek), and initiating capture efforts at leks regardless of the number of males observed. This capture strategy also increased the biological independence among study birds and strengthened our inferential abilities.

We attempted to monitor radio-collared hens at least once per week from April–September and twice per month from October–March. Occasionally hens were monitored less

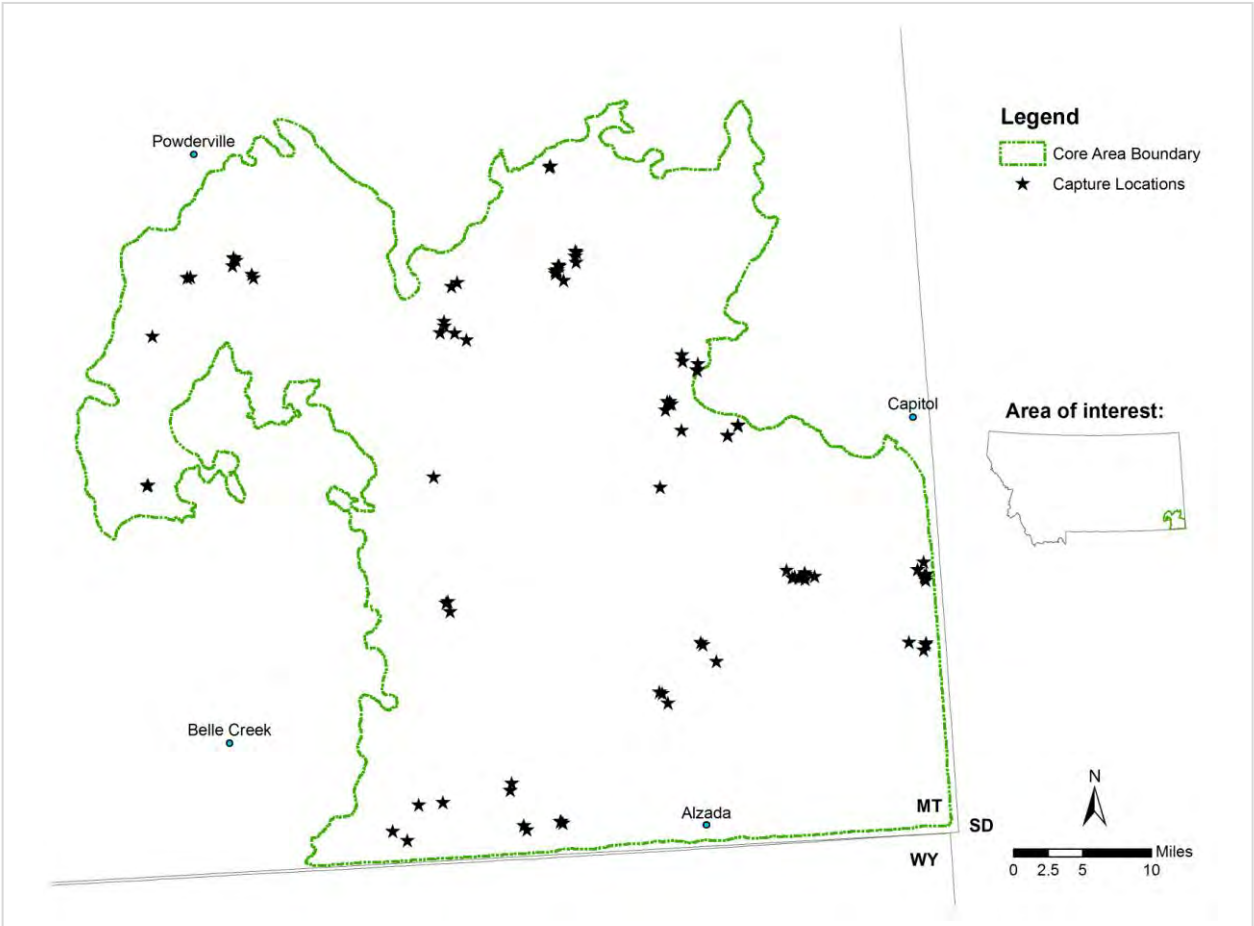


Figure 1.5. Capture locations for 94 radio-collared sage-grouse hens in the Southeast Montana Sage-Grouse Core Area. Each star represents 1–3 hens.

frequently due to severe weather events or logistical constraints. We used telemetry homing techniques (Samuel and Fuller 1996) to locate hens on the ground from April–September. We conducted telemetry flights when hens could not be located on the ground and to locate all hens from October–March. At each location, we recorded status (e.g., live, dead, nesting), GPS location, habitat information, and other pertinent notes.



– 2 –

Nest Success & Vegetation





INTRODUCTION

Nest success is one of the most important parameters driving population growth rates for sage-grouse (Taylor et al. 2010). Nest success varies among individual populations of sage-grouse and years, and may be influenced by land management and development activities (Connelly et al. 2011*a*). Therefore, it is necessary to quantify sage-grouse nest success and identify factors that may influence or limit nest success within sage-grouse core areas in order to better understand local population dynamics and make recommendations to improve nest success.

Sage-grouse nest success may be influenced by a variety of factors that land managers are unable to control such as climate, annual weather and existing levels of habitat fragmentation and development. However, land managers may have the ability to influence future land use and development activities. Two common practices to protect nesting sage-grouse and improve nest success are vegetation management and restrictions on development activities. Kevin Dougherty (University of Montana, unpublished data *in* Taylor et al. 2010) demonstrated that a 2 inch increase in grass height could result in a 10% increase in nest success, which could translate into an 8% increase in annual population growth (Taylor et al. 2010). Therefore, managed grazing is one of the few tools available for land managers to improve rates of nest success and facilitate sage-grouse population growth (Taylor et al. 2010). Timing restrictions to protect breeding and nesting sage-grouse from disturbance due to noise and activity associated with development typically begin March 1 and end June 15, but nesting season dates vary among sage-grouse populations (Schroeder et al. 1999, Gregg 2006). Therefore, quantifying nesting season dates and adjusting timing restrictions accordingly may minimize impacts of development on nesting grouse, as long as development activities do not result in long-term habitat loss, fragmentation, or degradation.

We quantified nesting season dates, nesting vital rates (nest initiation and success), fates of failed nests, nest site vegetation, and livestock occurrence at nest sites. We also investigated the influence of vegetation, livestock occurrence, weather, and other factors (e.g., hen age) on sage-grouse nest success. The resulting information will allow managers to better understand sage-grouse nest success within the Core Area (Fig. 1.2), identify factors that

influence success, and make appropriate management recommendations. It also provides valuable site-specific baseline data for comparison with other studies and the Core Area in the future.

METHODS

Nest monitoring

We monitored nests each spring from 2010–2012. We tracked hens at least once weekly using radiotelemetry equipment to locate nests and visually confirmed that hens were nesting from a distance of 15–20 yards. We estimated incubation initiation for each nest as the middle date between the last observation of a hen off a nest and the first observation of the same hen on a nest. For 8 nests with a long interval between observations (e.g., if a hen could not be located and was later found on a nest), we flushed hens and floated eggs to estimate incubation stage based on a 27 day incubation period (Westerkov 1950, Schroeder et al. 1999). This technique was necessary to accurately calculate dates for incubation initiation, but may cause some hens to abandon nests (Moynahan et al. 2007, Connelly et al. 2011*a*). Thus, we revisited flushed hens the following day to ensure that any researcher-caused nest abandonment was detected; no hens abandoned nests due to this technique. Once incubation was confirmed, we monitored nests at least weekly from >75 yards until hatch or nest failure. We classified failed nests as depredated (empty/destroyed nest bowl or hen dead) or abandoned (clutch intact and hen alive). We considered nests successful if at least one egg hatched determined by the presence of eggshells with detached membranes (Klebenow 1969). When nest bowls were undisturbed following a successful hatch, we counted the clutch size. We also noted whether livestock were present in the pasture where the nest occurred.

Vegetation sampling

We quantified vegetation structure at and adjacent to nest locations using protocol consistent with sage-grouse research elsewhere (e.g., Connelly et al. 2000*b*, Hagen et al. 2007, C. Wambolt, Montana State University, unpublished). We quantified shrub and herbaceous

vegetation structure along 2 perpendicular 98-ft line transects centered on nest bowls running from north to south and from east to west. We recorded the species, height, and maximum width of nest shrubs. We measured canopy cover of live shrubs using the line-intercept method (Canfield 1941, Connelly et al. 2003). We calculated shrub density by counting shrubs >6 inches in crown width within 3.3-ft of transects. We also measured the height of the nearest shrub at 3.3-ft intervals along the transect line. We measured herbaceous horizontal cover by placing 8 x 16 inch frames (Daubenmire 1959) at 10-ft intervals along line transects and recorded the percent cover (<5%, 5–25%, 25–50%, 50–75%, 75–95% or >95%) of 5 cover classes (live grass, residual vegetation, forb, cactus, and bare ground). We also measured the maximum live grass, forb, and the height of residual herbaceous vegetation within frames (residual height was only measured in 2011 and 2012). We measured visual obstruction at nest bowls by collecting height-density readings in each cardinal direction 13 ft from the nest bowl at a height of 3.3 ft following Robel et al. (1970).

Analyses

To evaluate the effectiveness of timing restrictions designed to benefit nesting hens, we present the median incubation initiation date and the length of the nesting season for each year of the study. We also present the median incubation initiation date of first nests by hen age class (yearling vs. adult). To better understand sage-grouse population dynamics within the Core Area and for comparison with other studies, we calculated several nesting vital rates. We calculated: 1) nest and renest initiation rates for each age class (yearling and adult) and year of the study, 2) mean, SE, and range for nest and renest clutch size, 3) apparent nest success (successful nests/all nest attempts) for each age class and nest attempt each year and overall apparent nest success for each year. Apparent nest success is useful for comparison with other studies, but is subject to bias (Mayfield 1961, Mayfield 1975). Maximum-likelihood estimators of daily survival rate are preferred to analyze nest survival data (Rotella 2010). We calculated the maximum-likelihood estimates for nest success using daily survival rate (DSR) of nests generated using program MARK (Rotella 2010) and a 27 day incubation period (Westerkov 1950, Schroeder et al. 1999). We present the percent of nests where livestock use was

concurrent with nesting and compared apparent nest success between nests in pastures with and without livestock present. We censored 2 nests from success analyses because we suspected researchers contributed to their failure. We also present fates of failed nests.

We provide descriptive information for nest site vegetation. For each nest shrub and stand variable, we calculated mean, SE, and range. The quantity and composition of herbaceous vegetation varies annually with precipitation. Therefore, we tested for differences in live grass height, forb height, and visual obstruction at nest sites among years using analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) multiple comparison test ($\alpha = 0.05$). We used a *t*-test to test for differences in the height of residual herbaceous vegetation between years ($\alpha = 0.05$). We present horizontal cover (mean and SE for each cover class) separately for each year. We used topography data in GIS to calculate the mean, SE, and range of elevation at nest locations.

We used an information-theoretic approach and the corrected Akaike Information Criterion (AIC_c; Burnham and Anderson 2002) to test among competing models for daily nest survival (DSR) in program MARK. We were interested in assessing 1) vegetation characteristics important for nest survival, 2) whether livestock presence influenced nest success, 3) if nest survival was related to local weather (average temperature and average daily rainfall during the nest survival period gathered from station USC00247034, NOAA, Ridgeway, MT), and 4) differences in nest survival between age classes. We also tested models for different nest success among years, nest attempt (first nest or renest), and calendar date. We compared all models against the null model of a constant DSR.

RESULTS

Nesting season dates

The median incubation initiation date (first nests and renests combined) was 2–3 weeks earlier in 2012 than 2010 or 2011 (Table 2.1). The total nesting season length, beginning with the earliest incubation initiation to the last hatch/depredation date, was similar in 2010 and 2011 (approximately 80 days), but shorter in 2012 (approximately 60 days; Table 2.1). The

nesting season began in mid-April each year, but lasted approximately a month longer in 2010 and 2011 than 2012 (Table 2.1). Yearling hens initiated first nests about a week later than adult hens in both 2010 and 2011 (adult median = 4/30/10 and 5/5/11; yearling median = 5/7/10 and 5/13/11). There were no yearlings in the study in 2012.

Table 2.1. Median incubation initiation date and nesting season length for radio-collared sage-grouse. Nesting season length is the earliest start of incubation to the last hatch/depredation date for each year.

Year	Incubation Initiation Date	Nesting Season Length (days)	
2010	5/2	4/16–7/4	(79)
2011	5/11	4/23–7/15	(83)
2012	4/20	4/9–6/10	(62)
All Years	4/30	4/9–7/15	(97)

Nesting vital rates

We summarized nesting results for 55 hens in 2010, 43 in 2011, and 27 in 2012. The percent of hens that initiated a first nest was variable but high for all years (≥85%; Table 2.2). The percent of hens (adult and yearling) that renested following an unsuccessful first nest was 42% across all years, although hens in 2012 renested at a lower rate than 2010 and 2011 (Table 2.2). Overall, 93% of adult hens and 87% of yearlings initiated a first nest, and 52% of adult hens and 21% of yearlings renested (Table 2.2). Two adult hens initiated a 3rd nest in 2011. Average clutch size was 7.92 eggs (SE = 0.16; range = 4–10) for first nests and 6.54 eggs (SE = 0.40; range = 4–9) for renests.

Table 2.2. Percent of radio-collared sage-grouse hens that initiated a first nest and renested by age class and year.

	% Nest Initiation	% Renest
Yearling	87% (80/86)	21% (5/24)
Adult	93% (34/39)	52% (23/42)
2010	87% (48/55)	40% (12/30)
2011	100% (43/43)	48% (13/27)
2012	85% (23/27)	29% (2/7)
Overall	91% (114/125)	42% (27/64)

Overall, apparent nest success across all years was 44% (62/142). Apparent nest success tended to be lower for yearlings than adults (Table 2.3). Success of first and second nest attempts was similar for all years combined (Table 2.3). Apparent nest success was higher in 2012 than 2010 and 2011. Maximum likelihood estimates for nest success were similar (within

Table 2.3. Apparent nest success (ANS; total successful nests/total nests) of radio-collared sage-grouse by age class and nest attempt each year, overall ANS each year, and maximum-likelihood estimates (MLE) with associated 95% confidence intervals (CI) for nest success each year. Maximum-likelihood estimates were not calculated by age class and nest attempt due to low sample size of subcategories.

	2010	2011	2012	All Years
Yearling	38% (10/26)	25% (3/12)		34%† (13/38)
Adult	47% (16/34)	36% (16/45)	68% (17/25)	47% (49/104)
Nest 1	38% (18/48)	36% (15/42)	70% (16/23)	43% (49/113)
Nest 2	67% (8/12)	31% (4/13)	50% (1/2)	48% (13/27)
Nest 3		0% (0/2)		0% (0/2)
ANS	43% (26/60)	33% (19/57)	68% (17/25)	44% (62/142)
MLE	42% (CI: 30–53%)	35% (CI: 23–48%)	60% (CI:34–76%)	42% (CI: 34–49%)

†Overall ANS for yearlings is probably not comparable to overall ANS for adults since no yearlings were followed in 2012, a year with high apparent nest success.

2%) to apparent nest success for 2010 and 2011, but 8% lower for 2012. Twenty-four percent (34/142) of nests were in pastures with cattle, 2% (4/142) with sheep, and 1% (2/142) with both cattle and sheep present. Apparent nest success was higher for nests in pastures with livestock present (59%; 24/41) than nests in pastures without livestock (38%; 38/100).

Fates of failed nests

All failed nests in 2010 and 2012, and the majority (87%; 33/38) of failed nests in 2011 were depredated. In 2011 the remaining nest failures were attributed to extreme precipitation and 100-year flood events, either by completely flooding the nest or causing the hen to abandon the nest after heavy rains. Flooding also reduced hatch rates in 2011, when one or more eggs were partially buried in mud, making it impossible for the egg to maintain adequate temperature for development, or for hens to turn the egg during incubation (Fig. 2.1). The magnitude of this effect was not estimated because nests commonly contain nonviable eggs and sample size of successful nests was low in 2011. However, >50% of successfully-hatched nests in 2011 contained at least one nonviable egg, compared with approximately 30% in other years of the study. No nests were trampled by livestock.



Figure 2.1. Nearly all nest failures were a result of depredation (left photo). However, a 100-year flood event in 2011 caused 9% of nests to fail and reduced the hatch rate for many nests when one or more eggs were partially buried in mud, making it impossible for the egg to maintain adequate temperature for development (right photo). The egg in the foreground of the photo on the right successfully hatched, but the 3 eggs behind did not.

Nest vegetation

Ninety percent (128/143) of nests were located beneath Wyoming big sagebrush, 7 nests were located in herbaceous vegetation with no shrub present, 4 nests beneath silver sagebrush, 3 beneath greasewood, and 1 nest beneath a silver buffaloberry (*Sherpherdia argentea*). Nest shrub and stand characteristics are presented in Table 2.4. Average grass height ($f_{2,140}$ = 31.94, P < 0.001) and average forb height ($f_{2,139}$ = 45.47, P < 0.001) differed among years and were lowest in 2012. The average height of residual herbaceous vegetation was greater in 2012 than 2011 (t_{43} = 2.02, P = 0.01; Table2.3). No differences were detected in visual obstruction ($f_{2,139}$ = 0.01, P = 0.99) at nest bowls among years (Table 2.4). Horizontal cover at nest stands was dominated by residual vegetation and bare ground in all years, but live grass and forb cover were higher in 2010 and 2011 than 2012 (Figure 2.2). Nest sites were located at an average elevation of 3442 ft (SE = 15 ft; range 2933–3907 ft).

Table 2.4. Vegetation characteristics of nest sites selected by radio-collared sage-grouse. The quantity and composition of herbaceous vegetation vary annually with precipitation. Therefore, means for herbaceous vegetation characteristics are presented separately when ANOVA and Tukey's HSD tests indicated differences (α = 0.05) among years.

Year	*n*	$\bar{x}$	SE	Range
Nest Shrub Height (in)				
All Years	138	21	0.5	5–48
Nest Shrub Maximum Width (in)				
All Years	138	46	4.6	7–114
Shrub Canopy Cover (%)				
All Years	143	16	1	1–54
Shrub Density (Shrubs /yd^2)				
All Years	143	0.93	0.03	0.03–2.25
Average Shrub Height (in)				
All Years	143	12.2	0.3	4.2–24.0
Average Grass Height (in)*				
2010[a]	59	10.4	0.2	7.0–17.6
2011[a]	59	11.1	0.3	7.0–17.6
2012[b]	25	7.1	0.3	5.0–10.0
All Years	143	10.1	0.2	5.0–17.6
Average Forb Height (in)*				
2010[a]	59	10.2	0.4	4.5–18.6
2011[b]	59	7.4	0.5	3.3–23.4
2012[c]	25	3	0.2	1.2–5.3
All Years	143	7.8	0.4	1.2–23.4
Average Residual Height (in)[#]				
2011[a]	59	7.6	0.3	3.5–14.2
2012[b]	25	9.1	0.5	4.9–15.5
All Years	84	8.1	0.3	3.5–15.5
Visual Obstruction (in)				
All Years	143	15.6	0.4	5.4–36.4

*Unlike letters ([a,b,c]) following years indicate statistically significant differences among years by ANOVA and Tukey's HSD test. However, these variables failed the homoscedastic assumption using Bartlett's test. Although ANOVA *P*-values for these variables were low, some discretion is needed with interpretation.

Residual height was not measured in 2010. Residual height differed between years by *t*-test.

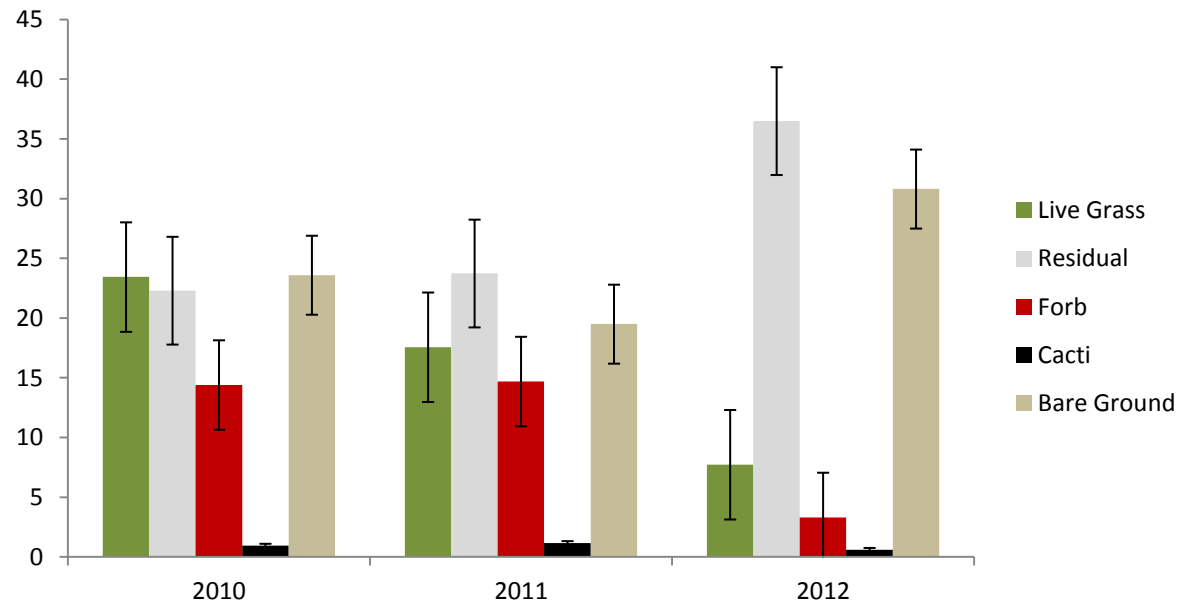


Figure 2.2. Mean and SE for percent horizontal cover of 5 vegetation cover classes estimated within Daubenmire (1959) frames along transects bisecting nests of radio-collared sage-grouse in southeastern Montana.

Factors influencing nest survival

Four models outperformed the model for constant DSR. These included 1) a model where DSR decreased with increasing total horizontal cover, 2) a model for DSR vs. calendar date, which indicated DSR was highest in the middle of the nesting season, 3) a binomial model where DSR tended to be higher in pastures with livestock present (95% confidence intervals overlapped), and a model where DSR tended to be higher in with increasing average temperature during the nest survival period (95% confidence intervals for the slope included zero). Models for hen age, nest attempt, year, and all other weather and vegetation covariates received less support than the model for constant DSR (Table 2.5).

Table 2.5. Ranking of model strengths for daily survival rates (DSR) of sage-grouse nests. Tested models included constant DSR, and models including covariates for several vegetative characteristics, livestock presence, weather conditions, hen age (yearling or adult), nest attempt (first nest or renest), calendar date, and year.

Model[A]	K	AIC_c	ΔAIC_c	w_i	Model structures & terms
Total Horizontal Cover	2	438.68	0.00	0.42	Logit-link of DSR = $\beta_1 + \beta_2$*x, where x is the sum of live grass + forb + residual horizontal cover. β_1 = 4.45 (95% CI = 3.62, 5.28), β_2 = -0.018 (95% CI = -0.031, -0.005).
Calendar Date	3	440.97	2.29	0.13	Logit-link of DSR = $\beta_1 + \beta_2$*x + β_3*x^2, where x is the calendar date. β_1 = 4.75 (95% CI = 3.59, 5.90), β_2 = -0.068 (95% CI = -0.129,-0.006), β_3 = 0.0007 (95% CI 0.000,0.001)
Livestock in Pasture	2	442.93	4.25	0.05	Binomial model where DSR for nests where livestock were present in the pasture = 0.977 (95% CI = 0.963,0.986), and DSR where no livestock were present = 0.965 (95% CI = 0.955,0.972)
Average temperature	2	443.03	4.36	0.05	Logit-link of DSR = $\beta_1 + \beta_2$*x , where x is the average temperature during the nest survival period. β_1 = 3.04 (2.55,3.53), β_2 = 0.07 (-0.02,0.2)
Constant DSR	1	443.75	5.08	0.03	DSR is constant throughout the nesting season, DSR = 0.968 (95% CI = 0.961, 0.974)
Average Grass Height	2	444.19	5.51	0.03	.
Year	3	444.53	5.86	0.02	.
Visual Obstruction	2	444.63	5.96	0.02	.
Sagebrush Canopy Cover	2	444.74	6.07	0.02	.
Forb Height	2	444.76	6.08	0.02	.
Hen Age	2	445.09	6.41	0.02	.
Average Rainfall	2	445.25	6.58	0.02	Model structures and terms are not presented for models with higher AIC_c than the model for constant DSR.
Residual Horizontal Cover	2	445.29	6.62	0.01	.
Shrub Density	2	445.34	6.67	0.01	.
Attempt (1st nest or renest)	2	445.58	6.90	0.01	.
Average Shrub Height	2	445.65	6.98	0.01	.
Nest Shrub Height	2	445.67	7.00	0.01	.
Nest Shrub Maximum Width	2	445.68	7.01	0.01	.

[A]K is the number of parameters included in the model, AIC_c is the Akaike Information Criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c from the top-performing model, and w_i is the Akaike weight which represents the probability of a model being the best approximating model of those evaluated (Burnham and Anderson 2002)

DISCUSSION

The nesting season was much shorter in 2012 (62 days) than 2010 and 2011 (≥79 days), due to high success of first nests and few renesting attempts. We attributed the difference primarily to drought conditions in 2012 (Appendix A). The lack of yearlings in the study during 2012 may have also contributed to a shorter nesting season, since yearlings tended to initiate first nests about a week later than adults. Similarly, the median incubation initiation date in 2012 (April 20) was nearly 2 weeks earlier than 2010 (May 2) and 3 weeks earlier than 2011 (May 11), and the nesting season lasted into early/mid-July during 2010 and 2011 but was complete by June 10 in 2012. Therefore, timing restrictions to benefit nesting grouse that end on June 15 may be effective during dry years, but during wetter years or years with a protracted nest season, the median start date for incubation is early to mid-May, and therefore only about 50% of nests would be expected to hatch by mid-June.

Nest initiation rates were higher in all years in the Core Area (Table 2.2; $\bar{x}$ = 91%) than averages from the eastern range of sage-grouse (82%, range = 67–100%; reviewed in Connelly et al. 2011*a*). Yearlings and adults had similar rates of initiation for first nests (87% and 93%, respectively), unlike studies elsewhere that documented lower nest initiation rates for yearlings (Connelly et al. 1993, Holloran et al. 2005, Moynahan et al. 2007). Conversely, yearlings had a much lower renesting probability than adults (23% and 52%, respectively). Others have suggested this may be due to later dates of first nest initiation for yearlings (Coggins 1998, Schroeder 1997, Moynahan et al. 2007). Overall, hens during the study had a higher renesting probability (42%) than the eastern range average (20%, range 9–38%; reviewed in Connelly et al. 2011*a*), even during 2012 when renesting rates were lowest (29%) during the study. High rates of nest and renest initiation in 2010 and 2011 may have been driven by above-average spring precipitation (Appendix A) which contributed to a long nesting season (79 and 83 days, respectively) and provided an abundance of protein-rich insects and forbs necessary for clutch production (Barnett and Crawford 1994, Coggins 1998, Gregg et al. 2006, Moynahan et al. 2007). Conversely, nest and renest initiation rates were lowest during drought year 2012 (Appendix A).

The average clutch size (7.6 eggs) was similar to that of nests from the eastern portion of the sage-grouse range (7.5 eggs; reviewed in Connelly et al. 2011*a*), northcentral Montana (8.3 eggs; Moynahan et al. 2007), northwestern South Dakota (8.3 eggs; Kaczor 2008), and southwest North Dakota (7.9 eggs; Herman-Brunson et al. 2009). Despite consistent clutch sizes produced, hatch rates were depressed in 2011 due to flood conditions. Extreme precipitation in 2011 caused some eggs to become partially buried in mud, making it impossible for eggs to maintain adequate temperature for development.

Apparent nest success varied among years (43% in 2010, 33% in 2011, and 68% in 2012). Maximum-likelihood estimates followed a similar trend, but 95% confidence intervals overlapped for all years (Table 2.3) and the model for different DSR among years performed poorly (Table 2.5). Low nest success in 2011 was driven by extreme precipitation and 100-year flood events, which caused 9% of nests to fail. Nest success is generally higher in wetter years (Coggins 1998, Gregg et al. 2006, Moynahan et al. 2007), but we suspect that flooding coupled with periods of below-average temperature in springs 2010 and 2011 (Appendix A) may have limited nest success in both years. However, the model for average daily rainfall performed poorly (Table 2.5), perhaps because rainfall has both positive (e.g., vegetation growth) and negative (e.g., flooding) effects that may have complex interactions with the nest site (e.g., topography at the nest site) or pattern of rainfall (e.g., gentle rain overnight versus a quick downpour). Also, rainfall is generally accompanied by cooler temperatures which may affect nest survival. We observed a trend for increasing DSR with increasing average temperature during the nest survival period, but 95% confidence intervals about the slope (β_2) overlapped zero (Table 2.5).

Vegetation, especially sagebrush canopy cover, residual vegetation, and live grass growth, is a primary factor that impacts sage-grouse nest success (e.g., Gregg et al. 1994, Connelly et al. 2000*b*, Holloran et al. 2005, Rebholz et al. 2009, Coates and Delehanty 2010), yet models relating nest shrub and stand characteristics to nest survival generally performed poorly (Table 2.5). The only vegetative model that outperformed the model for constant DSR was the sum of live grass + forb + residual horizontal cover. However, the slope of the resulting equation was negative, and solving the equation indicates that 5% increase in cover would

result in a 3% decrease in nest success. We suspect this counterintuitive outcome is a type II error. However, these results are a strong indication that herbaceous and shrub cover did not limit nest success during the study. Extreme moisture in 2010–11 resulted in tremendous growth of live vegetation, and abundant residual cover during 2012 (Table 2.4; Figure 2.2). Kevin Doherty (University of Montana *in* Taylor et al. 2010) found that a 2-inch increase in grass height (live and residual cover combined) would result in a 10% increase in nest success. The average live grass height surrounding nests in 2010 and 2011 study was toward the upper end of this graph (10.7 inches), and the maximum grass height was literally off the chart (17.6 inches; Table 2.4). Similarly, Gregg et al. (1994) found that nest success was greater when grass heights exceeded 7 inches, which was the average height of live grass during drought year 2012 (Table 2.4). This indicates that live grass height in the Core Area may be adequate for nesting sage-grouse even during years with low rainfall. However, grass heights taller than 7 inches are recommended to maximize nest success (K.E. Doherty, University of Montana *in* Taylor et al. 2010).

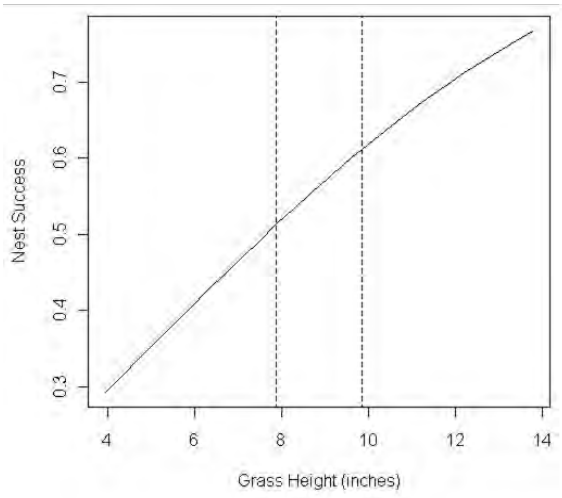


Figure 2.3. Results from other studies indicate that sage-grouse nests tend to be more successful when surrounding grass is taller. Data from the northern Powder River Basin (K.E. Doherty, University of Montana *in* Taylor et al. 2010).

Apparent nest success was higher for adults than yearlings (Table 2.3), but the difference was not statistically significant (Table 2.5), which is consistent with researchers elsewhere (Connelly et al. 2011*a*). Hen age may have contributed to higher nest success in 2012 since no yearlings were followed and surviving adult hens from previous years may be "wise" and more capable of successfully nesting (e.g. better nest shrub selection, better nesting area selection). However, the magnitude of this effect is likely small and secondary to the impact of favorable weather and abundant residual cover. Nest success was influenced by calendar date, with slightly higher rates of success in the middle of the nesting season (Table 2.5). Apparent nest success for renests varied among years due to low sample size, but overall

was similar to success for first nests (Table 2.3, Table 2.5), which differs from research conducted in central Montana where DSR was higher for renesting attempts than first nests (Sika 2006).

Overall apparent nest success for hens in the Core Area (43%) was similar to the average across the sage-grouse range (46%, range = 15–86%), but lower than the average for non-altered habitats (51%, range 24–71%; reviewed in Connelly et al. 2011*a*). Although extreme weather occurred during all years of the study, 2011 presented the most extreme conditions during the nesting season. In 2011, a 100-year flood event occurred during the nesting season that had a myriad of direct and indirect negative effects on nests and hens. Therefore, it may be reasonable to assume that average nest success in the Core Area would be more accurately estimated by averaging maximum-likelihood estimates for 2010 (42%; a cold, wet nesting season) and 2012 (60%; a warm, dry nesting season), while censoring nest success from extreme 2011. This results in 51% average nest success, which is equal to the average for unaltered habitats and probably a realistic estimate since the Core Area consists of largely intact habitat (Taylor et al. 2010).

Flooding drove between-year differences in apparent nest success, but depredation was the primary cause of nest failure in every year of the study. It is impossible to reliably assign a nest predator to species or class (e.g., aves or mammalia) based on sign left at the nest bowl (Coates et al. 2008). Potential nest predators that were observed in the study area include red fox (*Vulpes vulpes*), American badger (*Taxidea taxus*), bobcat (*Felis rufus*), coyote (*Canis latrans*), striped skunk (*Memphitis memphitis*), raccoon (*Procyon lotor*), domestic cat, common raven (*Corvus corax*), American crow (*Corvus brachyrhynchos*), and a variety of snake species. We suspect American badgers and striped skunks were responsible the majority of nest depredations. Both species were commonly observed during nighttime radio collaring efforts in the Core Area, and striped skunks followed by American badger were the most prevalent wildlife species observed at camera stations in a concurrent study in the Core Area (J. Alexander, St. Cloud State University, unpublished data). Common ravens and American crows do occur in the Core Area and potentially could have depredated some nests, but their abundance is low (based on field observations) and we suspect they were minor contributors to

nest predation. Although the majority of nest failures were due to predation, we do not presume that nest predation is a limiting factor for grouse within the Core Area because 1) for sage-grouse, as with other ground nesting birds, nest predation is a normal and expected occurrence, and 2) observed rates of nest success during our study were comparable with healthy sage-grouse populations elsewhere.

Maximum-likelihood models indicated a trend for increased DSR for nests in pastures with livestock present concurrent with the nest, and apparent nest success was higher for nests in pastures with livestock (59%) than pastures without livestock (38%). Additionally, we observed no direct negative impacts (e.g., trampling of nests) of livestock on nesting grouse. A similar trend has occasionally been reported for other prairie nesting birds. For example, Kirby and Grosz (1995) reported 25% higher nest success for sharp-tailed grouse (*Tympanuchus phasianellus*) in grazed than ungrazed pastures and Barker et al. (1990) reported 24% higher nest success for waterfowl nesting in twice-over rotationally-grazed pastures than idle pastures. Kirby and Grosz (1995) suggested this effect may have been a the result of behavioral avoidance of livestock by predators, or that grazing pastures reduced cover for predators, and that conversely the seclusion and cover provided by ungrazed areas may attract greater numbers of nest predators. Higher nest success in pastures with livestock may also reflect predator control efforts in areas with livestock, or predators focusing on alternate food sources (e.g., afterbirth) in areas with livestock. This effect was probably not an artifact of ranchers turning cattle into pastures that contain the best cover early in the season, because our results indicated that nest success was not related to vegetative characteristics. Regardless of the mechanism, a trend for higher nest success in grazed pastures coupled with no indication of vegetation structure limiting nest success are strong indicators that ranching activities that are occurring in the Core Area are not detrimental to nesting grouse. Overall, results from our study concur with research elsewhere that managed grazing is compatible with sage-grouse conservation, but we caution that we did not rigorously quantify the complex interrelationships among grazing, vegetation and sage-grouse nest success.



- 3 -

Brood Success & Vegetation





INTRODUCTION

Chick survival during the early brood-rearing period is one of the most influential and most variable population parameters for sage-grouse (Gregg et al. 2007, Connelly et al. 2011*b*, Taylor et al. 2012). Taylor et al. (2012) demonstrated that chick survival is the second most influential vital rate, behind hen survival, that influences population growth rates for sage-grouse, and that chick survival may account for >22% of the variation in population growth rates. Chick survival rates range from 12–50% for the first 18–51 days post-hatch and brood success (the percent of successfully-hatched broods where ≥1 chick survives past the early brood-rearing period) ranges from 21–100% (reviewed *in* Sika 2006). One reason for this variability is that chick survival is highly dependent on weather conditions. Young chicks (<2 weeks old) cannot thermoregulate independently and may succumb to exposure during cold, wet weather (Patterson 1952, Wallestad 1975). Further, chick survival is heavily influenced by forage (forbs and insects) availability and cover from predators, both of which are influenced by the timing and amount of precipitation. Although land managers cannot control precipitation, they can influence forage and cover available for brood-rearing sage-grouse through land management practices (e.g., grazing prescriptions) that improve vegetation structure and composition.

In order to improve our understanding of local sage-grouse population dynamics and make recommendations to improve chick survival rates, our objectives were to quantify brood-rearing dates, vital rates, brood site vegetation, and livestock occurrence at brood-rearing sites. The resulting information will allow managers to better understand sage-grouse brood success within the Core Area (Fig. 1.2), identify factors that influence success, and make appropriate management recommendations. It also provides valuable site-specific baseline data for comparison with other studies and the Core Area in the future.

METHODS

Brood monitoring

We monitored brood success at 14 and 30 days post-hatch. We conducted daytime flush counts at 14 days post-hatch and considered the brood successful if at least one chick was observed or hen behavior (e.g., vocalizing and walking off rather than flushing) suggested chicks were present. Broods were assumed failed if hens were observed with other breeding-aged birds on or before 14 days post-hatch. When brood presence was uncertain at 14 days, we returned at night when chicks roost with the hen to verify brood status. We did not attempt to get accurate brood counts at 14 days because 1) sage-grouse chicks are difficult to detect in daytime flush counts (Huwer 2004), and 2) two week old chicks were often fully concealed by brood hens at night (Fig. 3.1). We conducted nighttime brood counts 30 days post-hatch. At this point, chicks can be accurately counted since they are large enough that they cannot be fully concealed beneath the hen.

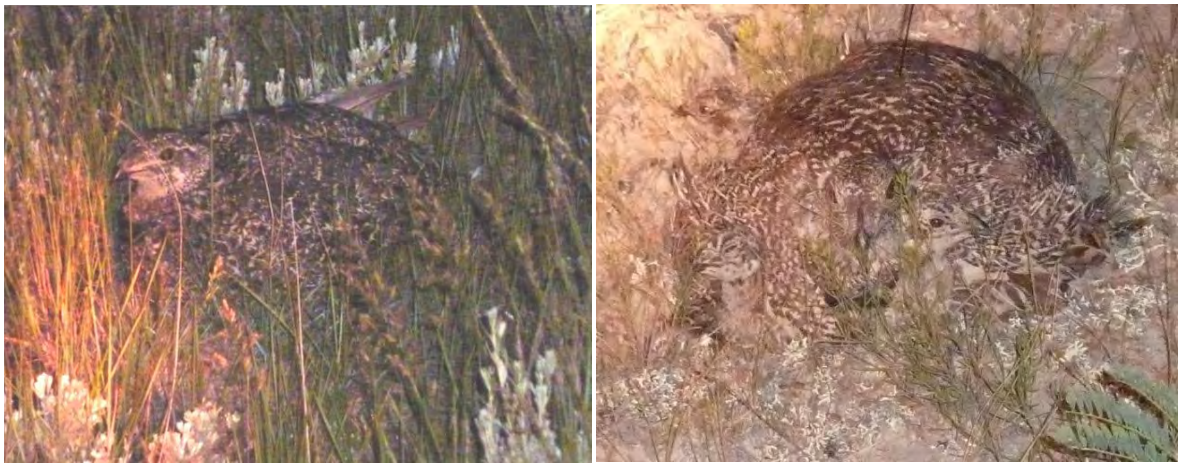


Figure 3.1. Left: this hen is brooding several chicks; 2 week old chicks were often fully concealed underneath brood hens at night. Right: as chicks approach 30 days old, they are too large to be fully concealed beneath the hen and can be accurately counted during nighttime brood counts.

Brood site vegetation

We quantified habitat characteristics at brood locations 14, 21, and 30 days post-hatch using 33-yd north to south transects centered on the brood location. We measured shrub canopy cover, shrub density, shrub height, grass height, forb height, height of residual herbaceous vegetation, horizontal cover, and livestock presence using vegetation sampling methods described in Chapter 2. Forb species richness and composition may be important for young chicks (Peterson 1970). Therefore, we determined the percent cover of each forb species within Daubenmire (1959) frames placed at every other 3.3-yd mark (e.g. 3.3, 9.9, 16.6 yd) along transects. To avoid disturbing broods, we delayed vegetation sampling until the next visit when hens and chicks had moved to a different location (within one week).

Analyses

We present the median and range of hatch dates for each year, and the percent of broods that hatched after June 15 (a common end date for timing restrictions). We calculated brood success and the average number of chicks per brood each year. We calculated chick survival by dividing the number of chicks that survived to 30 days by the number of eggs hatched. When nests were disturbed following hatch and it was impossible to accurately count the number of eggs that successfully hatched, we used the average number of viable eggs from other nests or renests as a surrogate. We calculated average chick production per hen by dividing the number of chicks that survived to 30 days by the number of hens that entered the nesting season.

We provide descriptive summaries of vegetation characteristics at brood locations. Because 14 and 21-day brood locations were determined during the day (foraging locations) and 30-day locations were determined at night (roosting locations), we report vegetation characteristics separately if daytime and nighttime locations differed by *t*-test for each variable. The quantity and composition of herbaceous vegetation varies annually with precipitation. Therefore, we tested for differences in live grass height and forb height at brood sites among years using analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) multiple comparison test. We used a *t*-test to test for differences in the height of residual

herbaceous vegetation between years. We present horizontal cover (mean and SE for each cover class) separately for each year.

To better understand factors influencing brood success, we compared 9 vegetative characteristics (shrub canopy cover, shrub density, shrub height, grass height, forb height, height of residual herbaceous vegetation, live grass horizontal cover, residual vegetation horizontal cover, and forb horizontal cover), and 2 weather variables (total precipitation and average temperature) between successful and failed broods using *t*-tests for unequal variance. We used Chi^2 tests for independence to test for differences in the proportion of successful broods between hen age classes (yearling or adult) and pastures with livestock concurrently present (cattle, sheep, or both). For 0–14 days post-hatch, we used data on vegetation and livestock presence collected at nest sites (Chapter 2) to approximate brood-rearing vegetation because 1) hens with broods tended to stay close to nests in the first 14 days post-hatch (Chapter 6), and 2) we did not conduct brood counts or measure vegetation until 14 days post-hatch thus post-hatch vegetation data for broods that failed during this time period were unavailable. We did not conduct tests for 14–30 days post-hatch because brood survival was ≥95% after 14 days (see results). We also calculated the percent of hens that used pastures with livestock in the first 30 days post-hatch and the total percent of brood locations that occurred in pastures with cattle and sheep concurrently present. All statistical tests were performed at $\alpha = 0.05$.

RESULTS

Brood-rearing dates & vital rates

During wet years 2010 and 2011, the median hatch date (first nests and renests combined) was during the first week of June, with 39% of hatches occurring after June 15 (Table 3.1, Fig. 3.2). During drought year 2012, the median hatch date was May 14. The early brood-rearing period during all years extended well past June 15 (Fig. 3.2).

Table 3.1. Median and range of hatch dates for radio-collared sage-grouse in southeastern Montana.

	Hatch Date	
Year	Median	Range
2010	June 3	May 18–July 4
2011	June 4	May 20–July 8
2012	May 14	May 6–June 10
All Years	June 1	May 6–July 8

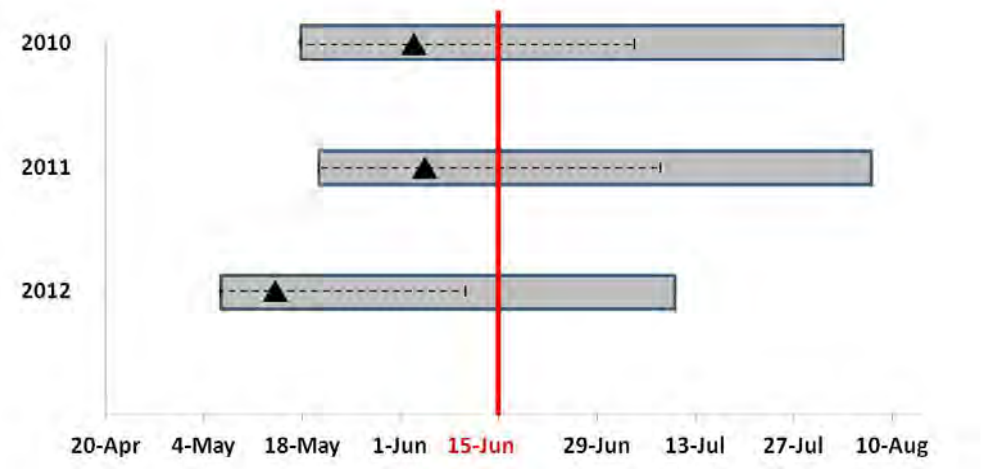


Figure 3.2. Range of hatch dates (dashed lines), median hatch date (triangles), and early brood-rearing period (hatch + 30 days; shaded boxes) for radio-collared sage-grouse in southeastern Montana. During wet years 2010–11, 36% (16/45) of hatches and the bulk of the early brood-rearing period occurred after June 15 (vertical red line). During drought year 2012, all nests were complete by June 10 but the early brood-rearing period extended into mid-July.

Brood success was similar among years ($\bar{x}$ = 65%; Table 3.2). Most of the broods that failed (86%; 19/22) did so during the first 14 days (Table 3.2). Three broods that had surviving chicks at 14 days were considered failed because the hen was killed before the brood reached 30 days old. No other broods failed between 14 and 30 days. Chick production was higher in 2010 and 2012 than 2011, however overall chick survival was similar among years (Table 3.3).

Table 3.2. Brood success for radio-collared sage-grouse in southeastern Montana. A brood was considered successful if ≥1 chick survived 30 days.

	Fate of Brood									
	0–14 days				14–30 days				30+ days	
	Fail		Hen Mortality		Fail		Hen Mortality		Success[a]	
Year	n	%	n	%	n	%	n	%	n	%
2010	6	23%	1	4%	0	0%	3	12%	16	62%
2011	5	26%	1	5%	0	0%	0	0%	13	68%
2012	5	29%	1	6%	0	0%	0	0%	11	65%
All Years	16	26%	3	5%	0	0%	3	5%	40	65%

Table 3.3. Average number of chicks per successful brood at 30 days post-hatch, chick survival (chicks that survived 30 days / total eggs hatched), and chick production per hen (total number of chicks that survived 30 days / total number of hens that began the nesting season) for radio-collared sage-grouse in southeastern Montana.

Year	Chicks per brood	Chick survival	Chick production per hen
2010	2.9	28%	0.87
2011	2.4	29%	0.72
2012	3.1	31%	1.14
All years	2.8	29%	0.88

Brood site vegetation

The average shrub height differed between daytime brood locations and nighttime roost locations (t_{75} = 1.99, P = 0.01), but no difference was detected in other shrub or vegetative characteristics between day and night locations ($t_{58} \geq 2.00$, $P \geq 0.50$; Tables 3.4 and 3.5). Live grass and forb height differed among years ($f_{2,112} \geq 19.61$, $P < 0.01$), but no difference in the height of residual herbaceous vegetation was detected between years (t_{55} = 2.00, P = 0.31; Table 3.5). Live grass comprised >20% of horizontal cover at brood-rearing locations in 2010 and 2011, but <10% of horizontal cover in 2012 (Fig. 3.3). Similarly, forbs comprised approximately 15% horizontal cover during 2010 and 2011 but <5% during 2012. Residual vegetation remaining from wet year 2011 comprised nearly 45% of ground cover in 2012, but <25% in 2010 and 2011.

Table 3.4. Shrub characteristics at sage-grouse brood-rearing locations. Average shrub height differed between daytime and nighttime locations (*P* = 0.01).

	Day/Night[a]	*n*	$\bar{x}$	SE	Range
Shrub Canopy Cover (%)	ND	114	8.1	0.1	0.0–48.5
Shrub Height (in)	Day	77	12.2	0.6	4.1–27.2
	Night	37	9.5	0.7	4.4–20.1
Shrub Density (shrub/yd^2)	ND	116	0.64	0.05	0.00–3.19

[a]ND = no difference between day and night locations ($P \geq 0.50$) by *t* test.

Table 3.5. Vegetative characteristics at sage-grouse brood-rearing locations. Live grass and forb height differed among years (*P* < 0.01) due to varied annual precipitation. No differences in vegetative characteristics between daytime locations and night roosting locations were detected by t tests (*P* ≥ 0.67).

	Year[A,B]	*n*	$\bar{x}$	SE	Range
Live Grass Height (in)[A]	2010	48	11.3	0.5	6.7–19.1
	2011	39	13.0	0.6	7.4–22.8
	2012	29	8.0	0.4	0.4–14.4
Forb Height (in)[A]	2010	48	13.3	0.6	6.4–26.4
	2011	38	7.8	0.7	0.8–24.7
	2012	28	3.2	0.4	1.2–9.7
Residual Vegetation Height (in)	ND	67	8.0	0.4	8.0–18.1

[A] Means for all years differ by analysis of variance and Tukey's Honestly Significant Difference Multiple Comparison Test (α = 0.05).
[B] ND = no difference between years (*P*= 0.31) by t test. Residual vegetation was not measured in 2010.

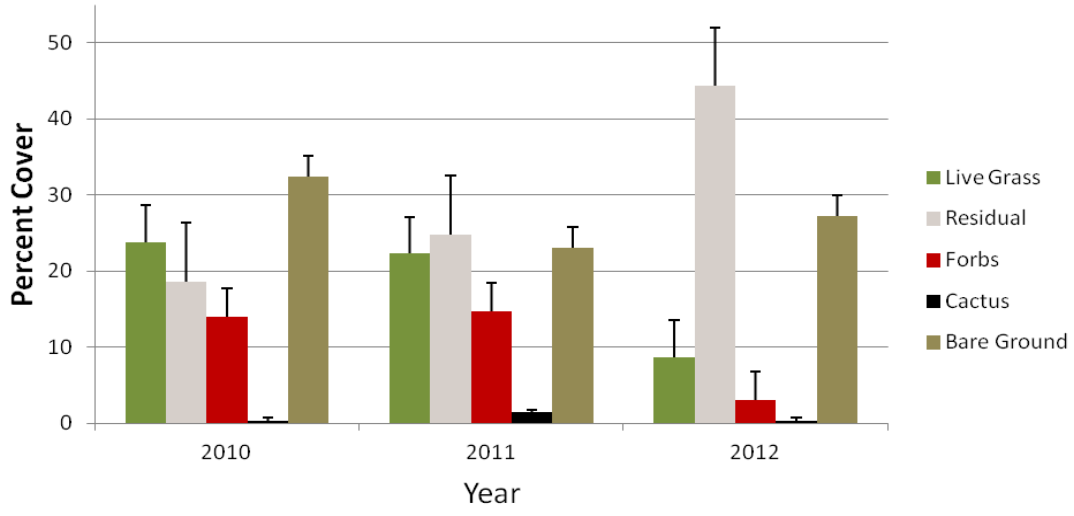


Figure 3.3. Average percent horizontal cover for 5 habitat variables measured within Daubenmire (1959) frames along transects at sage-grouse brood-rearing locations, 2010–2012.

Forb species richness at brood-rearing locations was highest during a year of extreme precipitation (2011) and lowest during drought (2012; Table 3.6, Appendix A). Percent occurrence and percent cover of common species at brood sites are listed in Table 3.7, and all forb species at brood-rearing locations are listed in Table 3.8. Example brood-rearing locations are pictured in Figure 3.4.

Table 3.6. Forb species richness at sage-grouse brood-rearing locations was highest during a year of extreme precipitation (2011) and lowest during drought (2012).

Year	N	$\bar{x}$	SE	Range
2010	48	4.3	0.4	1–13
2011	39	6.3	0.4	2–11
2012	29	3.3	0.3	0–7
All Years	116	4.7	0.2	0–13

Factors influencing brood success

Horizontal cover of forbs was greater for successful ($\bar{x}$ = 12.2% cover, SE = 1.3%) than failed broods ($\bar{x}$ =7.9% cover, SE = 1.3%; t_{50} = 2.37, P = 0.02), and the height of residual herbaceous vegetation was lower for successful ($\bar{x}$ = 7.2 in, SE = 0.5 in) than failed broods ($\bar{x}$ = 9.2 in, SE = 0.6 in; t_{26} = 2.65, P = 0.01). Shrub canopy cover, shrub density, shrub height, grass height, forb height, live grass horizontal cover, residual vegetation horizontal cover, total precipitation and average temperature did not differ between successful and failed broods ($t \leq 0.89$, $P \geq 0.37$). Brood success did not differ between yearlings and adults ($\chi^2 = 0.86$, df = 1, P = 0.36). There was a trend for higher brood success from 0–14 days post-hatch for broods hatched in pastures with livestock concurrently present (79%; 19/24) than in pastures without livestock (61%; 23/38; $\chi^2 = 2.97$, df = 1, P = 0.08). Seventy-one percent (30/42) of brood hens used pastures concurrently with livestock at some point between hatch and 30 days post-hatch, and 47% (55/116) of brood locations were in pastures with livestock concurrently present (41% cattle, 6% sheep).

Table 3.7. Percent occurrence (%Occ) of 7 common forb species at 116 sage-grouse brood-rearing locations and average percent horizontal cover (%HC) of each species where it occurred. All other species occurred at <15% of brood-rearing locations and are listed in Table 3.8.

	2010			2011			2012			All Years		
		%HC			%HC			%HC			%HC	
	%Occ	$\bar{x}$	SE	%Occ	$\bar{x}$	SE	%Occ	$\bar{x}$	SE	%Occ	$\bar{x}$	SE
Common Dandelion (*Taraxacum officinale*)	72.9	5.1	0.7	69.2	4.5	0.8	69.0	1.8	0.4	70.7	4.1	0.4
Common Yarrow (*Achillea millefolium*)	35.4	3.3	0.9	46.2	3.1	0.6	55.2	1.4	0.3	44.0	2.6	0.4
Vetch (e.g., *Astragalus spp.*)	33.3	2.7	0.6	48.7	3.5	0.6	31.0	1.1	0.2	37.9	2.7	0.4
Yellow Sweetclover (*Melilotus officinalis*)	33.3	4.7	1.0	48.7	7.3	1.6	10.3	1.0	0.3	32.8	5.7	0.9
Hood's Phlox (*Phlox hoodii*)	31.3	2.9	0.6	56.4	3.3	0.7	24.1	0.9	0.1	37.9	2.8	0.4
Wooly Plantain (*Plantago patagonica*)	12.5	2.5	0.0	38.5	3.2	0.5	6.9	2.5	0.0	19.8	3.0	0.3
Fringed Sagewort (*Artemisia frigida*)	18.8	7.4	2.0	12.8	8.8	2.8	13.8	3.5	1.0	15.5	6.9	1.3

Table 3.8. Percent occurrence (%Occ) for forb species occurring at <15% of brood-rearing locations for radio-collared sage-grouse in southeastern Montana, 2010–2012. Percent occurrence for common species (i.e., those that occurred at >15% of brood-rearing locations) are listed in Table 3.7.

Species	%Occ	Species	%Occ
Pepper grass (*Lipidium* spp.)	13.8	Fleabane (*Erigeron* spp.)	1.7
Scarlet globemallow (*Sphaeralrea coccinea*)	13.8	Northern Bedstraw (*Galium boreale*)	1.7
Bastard Toadflax (*Comandra umbellata*)	12.1	Praire coneflower (*Ratbida columnifera*)	1.7
Broom Snakeweed (*Gutierrezia sarothrae*)	11.2	Stemless Hymenoxys (*Hymenoxys acaulis*)	1.7
Breadroot Scurfpea (*Pediomelum esculentum*)	8.6	Canada lettuce (*Lactuca canadensis*)	0.9
Desert Biscuitroot (*Lomatium foeniculaceum*)	8.6	Canadian horseweed (*Conyza canadensis*)	0.9
Saltbush (*Atriplex* spp.)	6.9	Field pennycress (*Thlaspi arvense*)	0.9
Field cottonrose (*Logfia arvensis*)	6.0	Goldenpea (*Thermopsis rhombifolia*)	0.9
Salsify/Goat's beard (*Tragopogon dubius*)	6.0	Gumbo evening primrose (*Oenothera caespitosa*)	0.9
Dense clubmoss (*Selaginella densa*)	5.2	Hairy goldenaster (*Heterotheca villosa*)	0.9
White locoweed (*Astragalus* spp.)	5.2	Indian blanket flower (*Gaillardia pulchella*)	0.9
White Milkwort (*Polygala alba*)	5.2	Lambstongue groundsel (*Senecio integerrimus*)	0.9
Wild Onion (*Allium* spp.)	5.2	leafy phlox (*Phlox alyssifolia*)	0.9
Goldenrod (*Solidago* spp.)	4.3	Miner's candle (*Cryptantha virgata*)	0.9
Many flowered aster (*Symphyotrichum ericoides*)	4.3	Mule's ear (*Wyethia helianthoides*)	0.9
Scarlet Guaria (*Guaria coccinea*)	4.3	Oppositeleaf bahia (*Picradeniopsis oppositifolia*)	0.9
Curly Dock (*Rumex crispus*)	3.4	Perennial Sow thistle (*Sonchus arvensis*)	0.9
Cudweed Sagewort (*Artemisia ludoviciana*)	2.6	Prairie Chickweed (*Cerastium arvense*)	0.9
Field Pussytoes (*Antennaria neglecta*)	2.6	Purple loosetrife (*Lythrum salicaria*)	0.9
Meadow Deathcamas (*Zigadensu venonosus*)	2.6	Rabbit Tobacco (*Gnaphalium obtusifolium*)	0.9
Slimflower scurfpea (*Psoralidium tenuiflorum*)	2.6	Ragweed (*Ambrosia* spp.)	0.9
Smartweed (*Polygonym* spp.)	2.6	Rough false pennyroyal (*Hedeoma hispida*)	0.9
Stoneseed (*Lithospermum* spp.)	2.6	Twogrooved poisonvetch (*Astragalus bisulcatus*)	0.9
White clover (*Trifolium repens*)	2.6	Violet (*Viola* spp.)	0.9
Alfalfa (*Medicago sativa*)	2.6	White prairie aster (*Symphyotrichum falcatum*)	0.9



Figure 3.4. Example brood-rearing locations for radio-collared greater sage-grouse. A typical brood-rearing location had about 8% shrub canopy cover (upper right photo). Some hens raised chicks in areas with very little sagebrush (lower photo) whereas others used areas with moderate (upper left photo) to dense sagebrush. The range of sagebrush canopy cover at brood-rearing locations was 0–48%. Sagebrush can provide thermal and hiding cover for sage-grouse chicks (middle right photo).

DISCUSSION

Wet conditions during 2010 and 2011 resulted in a protracted nesting season, with 36% of hatches and the bulk of the early brood-rearing period occurring after June 15. Nesting season 2010 occurred during a drought year following a mild winter (Appendix A), and all nests hatched by June 15 but the early brood-rearing period extended to July 10. Therefore, timing restrictions that end on June 15 will not benefit later nesting hens or young broods in most years. Timing of hatch and the early brood-rearing period during a "normal" year might be expected to be intermediate between wet years 2010 and 2011 and drought year 2012, with a median hatch date of approximately May 24 and latest hatch date of June 24. If timing restrictions were maintained until July 15, it would be reasonable to assume that in most years nearly all nesting would be complete, nearly all chicks would be >2 weeks old, and more than half of broods would have reached 30 days. Extending timing restrictions to benefit young sage-grouse chicks may be important because most chick mortality occurs within the first 4 weeks after hatching (Gregg et al. 2007, Dahlgren et al. 2010*a*), and chick survival is one of the most important parameters influencing population growth rates for sage-grouse (Taylor et al. 2010). However, timing restrictions are only effective for minimally invasive, short duration projects and cannot be expected to offset the impacts of long-term habitat loss, fragmentation, or degradation.

Of 62 broods, 40 (65%) had chicks survive to 30 days. One brood hen mortality occurred between hatching and 14 days in each of the 3 years, and 3 brood hens died between 14 and 30 days post-hatch in 2010. Sage-grouse hens commonly mix broods and adopt orphans (Dahlgren et al. 2010*a*), and consequently it is possible that some orphaned chicks in our study survived. Survival of orphaned chicks that are less than 10 days old is probably low due to the solitary nature of hens with young chicks (Dalke et al. 1963), but survival of broods over 10 days old may approach 100% because hen locations tend to overlap as chicks grow, and older chicks may survive several days without a brood hen before being adopted (Patterson 1952, Keppie 1977, Connelly et al. 2006). Further, spotlight counts are highly accurate but it is possible that detection was <100% during nighttime brood counts (Dahlgren et al. 2010*b*). Thus, reported values for brood success and chick production are minimum estimates.

Comparison of brood and chick survival among studies is confounded because researchers have used different field methods and intervals (ranging from 18–51 days post-hatch) to quantify brood and chick survival (reviewed in Connelly et al. 2011*a*). However, it may be reasonable to compare estimates for brood and chick survival for different durations post-hatch given that chick mortality is highest immediately post-hatch and survival is expected to be high during the period of discrepancy (Sika 2006, Gregg et al. 2007). Our estimate of 65% for brood survival is in the middle of the range reported by other researchers (21–100%; reviewed *in* Sika 2006). It was above the range reported from northwestern South Dakota (32–52%; Kaczor 2008) and southwestern North Dakota (34–42%; Herman-Brunson 2007), at the high end of the range reported for northcentral Montana (21–76%; Moynahan 2004), and below the range reported from central Montana (71–84%; Sika 2006). Similarly, our estimate for chick survival (29%) is in the middle of the range reported by other researchers (12–50%; reviewed in Connelly et al. 2011*a*).

Brood and chick survival vary among years and study areas (Connelly et al. 2011*a*) but were remarkably consistent between very wet and very dry years in our study (Tables 3.2 and 3.3, Appendix A). Cold, wet weather may be devastating to young chicks because they cannot thermoregulate independently (Patterson 1952, Wallestad 1975), thus we expected brood and chick survival would be related to weather variables and lower in 2010 and 2011 than 2012. However, when food is abundant chicks do not need to spend as much time and effort foraging and may avoid exposure by spending considerable time brooding during cold, rainy days (Zwickel 1967, Connelly et al. 2006). Abundant forbs and insects (especially grasshoppers; based on field observation) provided ample forage for chicks during wet years 2010 and 2011, and may have helped chicks survive in the face of harsh weather conditions. Conversely, weather for broods was favorable in 2012, but drought conditions resulted in low forb abundance and concomitantly insect abundance (Southwood and Cross 2002) which can limit brood survival (Peterson 1970, Drut et al. 1994*b*). Adequate cover (live vegetation in 2010 and 2011 and residual vegetation in 2012; Fig. 3.3) was available to broods during all years of the study, and may have contributed to similar rates of brood and chick survival among years.

Unlike brood and chick survival, chick production varied among years. Chick production is influenced by a variety of reproductive parameters including hen survival, nest success, hatch rates, and chick survival, and therefore represents a comprehensive measure of sage-grouse annual production. Chick production was lowest in 2011, which resulted from extreme moisture during that year (Appendix A) that caused lower nest success, reduced hatch rates (Fig 2.1), and therefore a lower average number of chicks per brood.

Brood-rearing sage-grouse tended to use open stands of sagebrush ($\bar{x}$ = 8% canopy cover), which is similar to studies elsewhere (e.g., Wallestad 1971, Connelly 1982). Brood success during the first 14 days post-hatch was not related to shrub characteristics, which suggests that adequate shrub cover was available for broods, or that shrub cover is secondary to other habitat features (e.g., forb availability) for brood survival. Shrub canopy cover and density were similar between day and night locations, but the average shrub height was slightly higher at daytime brood locations than nighttime roost locations. We suspect that slightly taller shrubs may offer better cover from avian predators during daylight hours.

Grass cover at brood-rearing sites was related to annual precipitation ($\bar{x}$ height: 8–13 in), but was not related to brood success. Researchers elsewhere have reported conflicting results, probably an artifact of location, soil type, grass composition, and grass availability. Some suggest that brood hens select areas with taller grass than random locations (e.g., $\bar{x}$ = 16.7 in, Aldridge and Brigham 2002), whereas others have reported that brood hens select areas with short grass (e.g., < 7 in, Sveum et al. 1998). Live and residual vegetation can provide valuable cover from predators but cover that is too dense can inhibit brood hens from detecting and escaping predators (Aldridge 2005, Gregg and Crawford 2009), and can also contribute to exposure-related death of chicks during cold, wet days (Patterson 1952), which may explain our counterintuitive finding that residual vegetation was shorter for successful broods. Optimal grass cover given these opposing effects is probably related to individual site characteristics, weather during the brood-rearing period, and the structure and composition of other vegetative components. Grass cover did not differ between successful and failed broods, which suggests grass cover was secondary to other habitat features (i.e., forbs).

Forbs comprised approximately 15% horizontal cover at brood sites during 2010 and 2011 but less than 5% during drought year 2012, and forb cover was higher for successful (12.2% cover) than failed (7.9% cover) broods. Sage-grouse researchers elsewhere have reported similar (7–14%) forb cover during early brood-rearing and the importance of forbs for chick survival (e.g., Schoenberg 1982, Drut et al. 1994*a,b*, Aldridge and Brigham 2002). As upland vegetation desiccates and senesces, brood hens tend to move to mesic areas with high (up to 41%) forb cover to meet the dietary requirements of chicks (e.g., Peterson 1970, Dunn and Braun 1986, Sveum et al. 1998). We did not quantify vegetation use during late brood-rearing due to logistic constraints, but we did observe a trend toward grouse using more mesic areas during late brood-rearing. Forty percent of locations were within 100 yards of a creek, pond, or wetland for late brood-rearing hens compared to 25% for broodless hens and 16% for early brood-rearing hens (see Chapter 6).

Similar to forb cover, forb species richness at brood-rearing locations was highest during a year of extreme precipitation (2011) and lowest during drought (2012; Table 3.6). Percent occurrence and cover of common species were fairly consistent among years (Table 3.7). We did not quantify forb availability at random sites. However, 2011 was a sweet clover "boom" year, and sweet clover was the dominant species in many parts of the study area (field observation, Fig. 3.5). Sweet clover was present at 49% of brood-rearing locations but only comprised an average 7% and maximum 16% cover where it occurred, indicating that areas of dense sweet clover were not preferred brood-rearing habitat (Fig. 3.5, Table 3.7).

Brood success was higher in pastures with livestock concurrently present (79%) than in pastures without livestock (61%). The mechanism for this is unknown; it may be a result of behavioral avoidance of livestock by predators (Kirby and Grosz 1995), or predator control efforts in areas with livestock. Extensive use of pastures concurrent with livestock is a strong indicator that brood hens did not avoid livestock, but nor did they exhibit strong selection for pastures with livestock. Over 70% of brood hens used pastures with livestock at some point during the first 30 days post-hatch (a rough idea of availability), but only 47% of brood-rearing locations were in pastures with livestock. Hens are probably selecting areas based on forage and cover for broods rather than simply livestock presence. Recently grazed pastures may be



Figure 3.5. Sweet clover dominated much of the landscape of the study area during 2011. Sweet clover was present at 49% of brood-rearing locations in 2011 but only comprised an average 7% and maximum 16% cover where it occurred, indicating that areas of dense sweet clover were probably not preferred brood-rearing habitat. However, sage-grouse did not avoid dense areas of sweet clover altogether and dense sweet clover can provide good hiding cover, as demonstrated by the broodless hen in the bottom of the photograph on the right.

attractive to brood hens because cattle in large summer pastures do not typically consume vegetation in a uniform fashion, resulting in a heterogeneous mix of open areas where chicks can forage interspersed with ungrazed areas that provide escape cover. Despite trends for higher nest (Chapter 2) and brood success in pastures with livestock, we do not suggest land managers increase livestock stocking rates throughout the Core Area because improper grazing can degrade cover and forage that are critical for sage-grouse survival and reproduction. It is well-documented that managed grazing can promote forb and grass diversity, healthy shrub communities, and overall rangeland health (e.g., McCarthy 2003). Our results provide further evidence that livestock presence on the landscape can benefit nesting and brood-rearing sage-grouse.



- 4 -

Hen Survival



INTRODUCTION

As with other upland game bird species, sage-grouse exhibit high reproductive capability and population levels are driven primarily by annual production (Crawford et al. 2004). However sage-grouse typically exhibit smaller average clutch sizes, lower renesting rates, and higher annual hen survival than other upland game birds. Thus sage-grouse populations are more dependent on survival rates than other upland game bird species (Saether and Bakke 2000, Connelly et al. 2011*a*, Taylor et al. 2012). Hen survival, chick survival, and nest success are the 3 vital rates that are the most significant drivers of sage-grouse population growth rates (Walker 2008, Dahlgren 2009, Taylor et al. 2012). Our goal was to quantify hen survival and identify sources of hen mortality for sage-grouse in the Core Area (Fig. 1.2).

METHODS

Radio collars were equipped with mortality signals that activate when collars are stationary for 4 or more hours. When hen mortalities occurred, we located carcasses as soon as possible to determine the cause of mortality and collect remains. When bones were crushed, or mammalian sign was observed at the kill site, we classified mortality as mammalian predation (Sika 2006). When only feathers remained, if bones and ligaments were stripped, or if raptor mutes were located near the carcass, we classified mortality as avian predation (Sika 2006). When evidence was insufficient to determine cause of death, we classified the mortality as unknown. We used known-fate models in program MARK (Cooch and White 2010) to estimate annual (March 1–February 28) survival (ϕ), as well as survival for 4 seasonal periods: breeding (March 1–April 15), nesting/brood-rearing (April 16–July 15), late summer/fall (July 16–October 31), and winter (November 1–February 28). These periods follow Swanson (2009) to allow for comparison of survival between studies in close geographic proximity. We tested whether survival differed between yearling and adult hens. We excluded 2009 data from known-fate analyses due to low sample size. We also provide summaries of cause-specific mortality.

RESULTS

The top-performing model for hen survival (season + different fall and winter 2010; Table 4.1) indicated survival varied among seasons but survival during late summer/fall and winter 2010 was lower than survival for the same periods in 2011 and 2012. This model was determined *a posteriori* based on seasonal survival rates in Table 4.2. In all years, hen survival was lowest during the nesting and brood-rearing period ($\bar{x}$ = 68%), and higher during other seasons ($\bar{x} \geq 90\%$) with the exception of late summer/fall and winter of 2010. Due to lower late summer/fall and winter survival in 2010, annual hen survival was lower in 2010–2011 (ϕ = 45%) than 2011–2012 (ϕ = 59%) or 2012–2013 (ϕ = 61%), but 95% confidence intervals overlapped (Table 4.2). Differentiating adults and yearlings did not improve survival models (Hen Age ΔAIC_c = 1385; Table 4.1).

Table 4.1. Ranking of model strengths (shown strongest to weakest) for hen survival in the Southeast Montana Sage-grouse Core Area. Models included constant survival among seasons and years, and models where survival varied with hen age (adult or yearling), seasons, years, both seasons and years, and among seasons with different survival during fall and winter 2010.

Model[A]	K	AIC_c	ΔAIC_c	w_i
Season + different fall and winter 2010[B]	6	522.6	0.0	0.87
Season	4	526.5	4.0	0.12
Season & Year	12	530.8	8.2	0.01
Constant	1	543.9	21.4	0.00
Year	3	544.8	22.2	0.00
Hen Age	1	1907.9	1385.3	0.00

[A]K is the number of parameters included in the model, AIC_c is the Akaike Information Criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c from the top-performing model, and w_i is the Akaike weight which represents the probability of a model being the best approximating model of those evaluated (Burnham and Anderson 2002)

[B]Model determined *a posteriori* based on patterns of seasonal survival in Table 4.2. We suspected a slight WNv outbreak in fall 2010 and winter 2010 was severe. All other models were determined *a priori*.

Table 4.2. Survival of radio-collared sage-grouse hens during breeding (March 1–April 15), nesting/brood-rearing (April 16–July 15), late summer/fall (July 16–October 31), winter (November 1–February 28), and annual survival (March 1–February 28). Survival (ϕ) and 95% confidence intervals (95% CI) were calculated using known-fate models in program MARK (Cooch and White 2010).

	Year							
	2010–2011		2011–2012		2012–2013		All Years	
Season	ϕ	95% CI*	ϕ	95% CI	ϕ	95% CI*	ϕ	95% CI
Breeding	100%	NC	97%	79–100%	100%	NC	99%	94–100%
Nesting/Brood-rearing	68%	54–78%	70%	54–81%	65%	44–80%	68%	59–75%
Late Summer/Fall	81%	65–91%	94%	77–98%	98%	84–100%	90%	83–95%
Winter	83%	67–92%	95%	82–99%	100%	NC	93%	86–96%
Annual Survival	*45%*	*32–57%*	*59%*	*44–71%*	*61%*	*41–77%*	*53%*	*44–61%*

*NC = not calculated; 95% CI's could not be calculated when survival was 100%

Mortality was due primarily to avian followed by mammalian predation (Fig. 4.1). Cause of mortality could not be determined for 24%, and a predator could not be assigned for 5% of mortalities. We suspect WNv for 2 (3%) carcasses found intact without indication of predation or other trauma. These mortalities occurred in late August 2010 and late June 2011. However, upon recovery, decomposition was too advanced to perform laboratory analyses. No mortalities were attributed to collision with fences or power lines. No other carcasses or collars were found near fences or power lines. No hunting mortalities occurred, nor did any collared grouse disappear (potentially harvested) during the hunting season (September 1–November 1 each year).

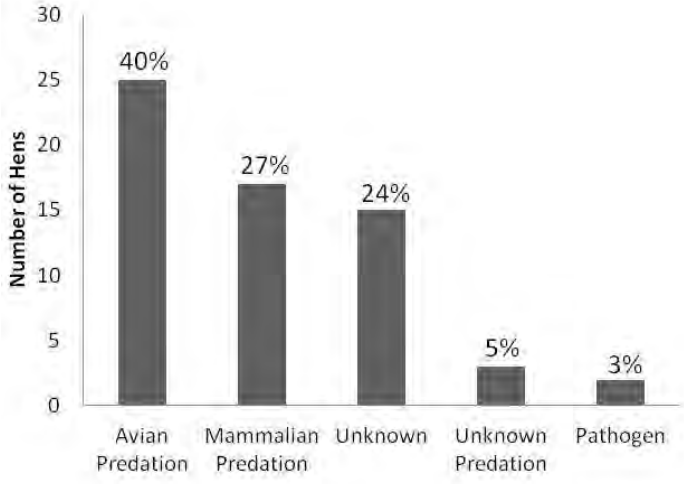


Figure 4.1. Cause-specific mortality for 62 radio-collared sage-grouse hens in southeastern Montana.

DISCUSSION

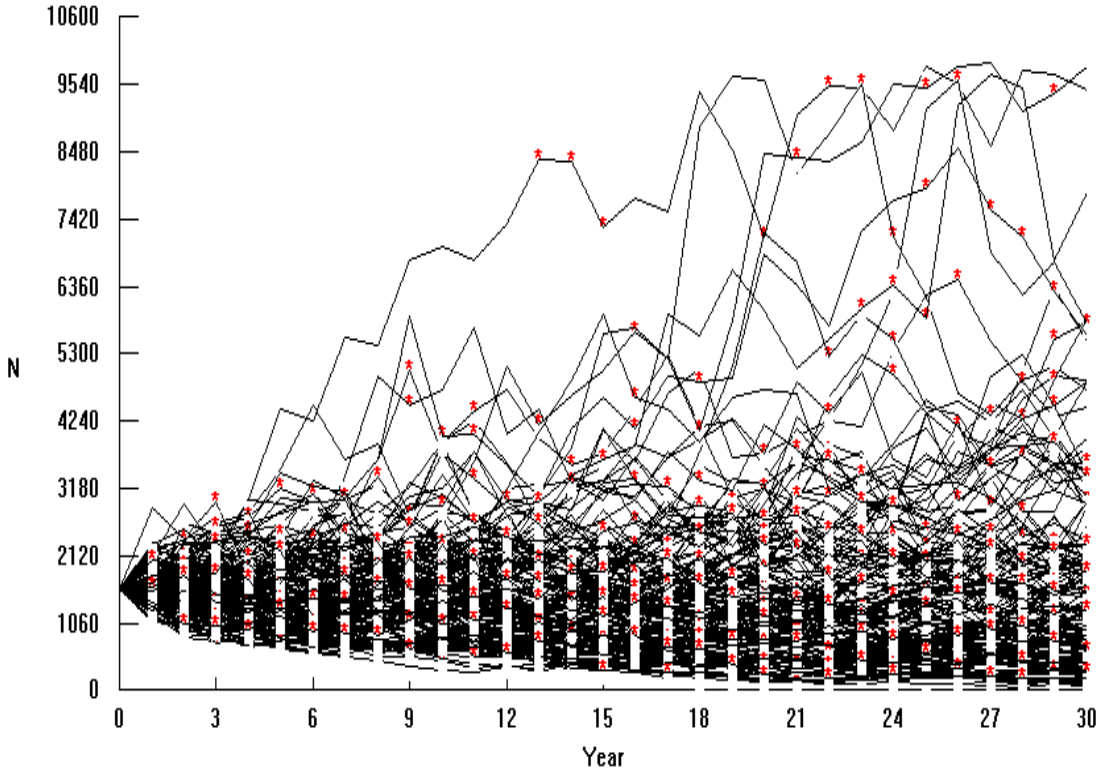
Annual hen survival in the Core Area during 2011–12 and 2012–13 (59 and 61%) was similar to average survival for sage-grouse hens reported by researchers elsewhere (average = 60%, range = 37–78% reviewed in Connelly et al. 2011*a*), but survival during 2010–11 was 45%. Lower annual survival in 2010–11 was driven by lower seasonal survival during late summer/fall and winter periods. For other seasons, survival was similar during all years of the study. West Nile virus can significantly reduce survival of sage-grouse during late summer to early fall, and mortalities resulting from WNv may be attributed to predation when neurological effects make hens more susceptible to predators (Swanson 2009, Naugle et al. 2004). West Nile virus was not documented in Montana during the study, but was detected adjacent to the Core Area in Butte County, South Dakota in 2010 (Centers for Disease Control 2013). Mortality due to WNv may explain the low late summer/fall survival (81%) in 2010 compared to 2011 and 2012 (94 and 98%). Six of 9 mortalities that occurred during late summer/fall 2010 occurred from late July to August, the peak period for WNv outbreaks. We did suspect WNv for one mortality in 2010. However, even though we observed an increase in hen mortality during this period, we did not see the drastic reduction in hen survival typical of WNv outbreaks. For example, annual survival of hens in areas of South Dakota adjacent to the Core Area plummeted from 78% in 2006 to 41% during the WNv outbreak in 2007 (Swanson 2009). On average, the virus may reduce late summer survival by 25% (Walker and Naugle 2011). Survival during late summer/fall 2010 in the Core Area was reduced by only 15%, perhaps due to decreased sage-grouse densities in the Core Area following the 2007 outbreak (Fig. 1.3) or environmental conditions that limited the severity of the potential WNv outbreak.

Survival of hens during severe winter 2010–11 (83%) was about 15% lower than winters 2011–12 and 2012–13 (95 and 100%). Overwinter survival for sage-grouse hens is generally high (88–100%; Wik 2002, Swanson 2009), but reduced survival during severe winters has been documented in northcentral Montana (99% survival during a mild winter vs. 91% survival during a severe winter; Moynahan et al. 2006). We suspect heavy snow cover during winter 2010–2011 reduced hiding cover, thermal cover, and forage available to grouse and also concentrated birds, making them particularly vulnerable to avian predators (Fig. 4.2).



Figure 4.2. Heavy snow cover during winter 2010–2011 reduced hiding cover and concentrated sage-grouse, making the flock of 40+ birds highly visible in an aerial photo on the left. In contrast, normal winter conditions result in a mosaic of vegetative cover and snow patches, and the single hen in the lower left corner of the right photo is much less conspicuous.

The majority of sage-grouse mortalities were due to predation, which was expected given that sage-grouse are a prey species. Mortality was due primarily to avian (≥40%) and mammalian (≥28%) predation. It is impossible to reliably assign a predator species based on remains, but potential avian predators on sage-grouse include Bald Eagles (*Haliaeetus leucocephalus*), Golden Eagles (*Aquila chrysaetos*), and a variety of hawk (Aves: falconiformes) species. Potential mammalian predators include red fox, bobcat, badger, and coyote among others. We do not suspect predation is limiting sage-grouse populations in the Core Area given observed rates of annual survival for 2011–12 and 2012–13 were normal for healthy sage-grouse populations (approximately 60%), and decreased survival during extreme winter events, as observed during the 2010–11 winter, is an expected but infrequent occurrence (Moynahan 2006, Appendix A).



- 5 -

Population Viability



INTRODUCTION

Population viability analysis (PVA) uses species characteristics (e.g., survival and reproduction rates), environmental variability, and stochasticity to model population health and probability of population persistence (Boyce 1992). Computer programs such as VORTEX (Lacy et al. 2003) make it possible to run thousands of iterations for different scenarios using species characteristics, environmental variability, and stochastic events (Fig. 5.1). Individual iterations are averaged to predict population growth rates and extinction probability for each scenario. Various scenarios can provide insight into critical life stages, or predict the impact of catastrophic events. Population viability analyses cannot be expected to yield exact population trajectories because it is impossible to reliably predict the future. For example, the quality and quantity of habitat may change, or unpredictable catastrophes such as fire, floods, or disease outbreaks may occur. Nevertheless, PVA is a useful tool to better understand the factors underlying population dynamics.

Taylor et al. (2010) conducted a robust PVA that included the Core Area (Fig. 1.2). They used a lek count-based approach to evaluate the impacts of stressors (tillage, energy development, and WNv outbreaks) on sage-grouse populations and a vital rate-based sensitivity analysis to explore which vital rates are most important to sage-grouse population

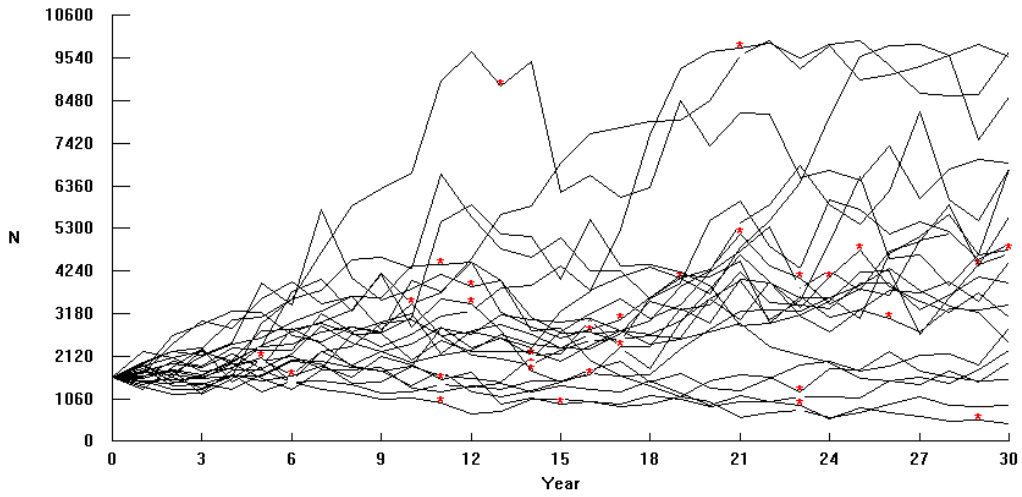


Figure 5.1. Example VORTEX (Lacy et al. 2003) simulation picturing several potential population trajectories, called iterations (black lines), for a single scenario. Individual iterations incorporate environmental variability and stochastic events. VORTEX runs thousands of iterations and averages them to predict population growth rates and extinction probabilities for individual scenarios.

growth rates. However, the population vital rates used in the analysis were derived from research projects completed outside of the Core Area. Our goal was to assess population viability for sage-grouse in the Core Area using locally-derived population vital rates. The resulting information will complement the broader results of Taylor et al. (2010).

METHODS

We used program VORTEX (Lacy et al. 2003, Miller and Lacy 2005) to run population viability simulations for several scenarios. We ran each scenario for 10,000 iterations over a 30 year period for a single population. We assumed no inbreeding depression was currently occurring. Sage-grouse reproductive rates and survival are influenced by annual cover conditions, so we ran models assuming environmental concordance of reproduction and survival (i.e., that good years for reproduction are also generally good years for survival).

Sage-grouse are polygynous with first reproduction at age one. We assumed a maximum age of reproduction of 10 years, based on the estimated maximum life span of sage-grouse (USFWS 2011). We used data from collared hens in the Core Area for percent breeding (the percent of hens entering the nesting season that hatched ≥ 1 egg) and offspring per brood (average number of successfully hatched eggs and associated SD; Table 5.1). We assumed a 50-50 sex ratio at birth. We estimated SD in percent breeding due to environmental variation using methods outlined in Rohlf and Sokal (1981) to calculate SD for small sample sizes (n = 3 years). We assumed demographic stochasticity was negligible because within-year sample sizes were large ($n \geq 27$).

We estimated mortality from birth to one year based on survival of chicks for early brood-rearing period from the Core Area (29%) multiplied by survival of chicks from late brood-rearing to one year (73–75%) from Taylor et al. (2010), which results in 22% survival. We estimated SD in first year mortality was approximately 4% based on consistent annual chick survival in the Core Area (see Chapter 3) and 95% confidence intervals presented in Taylor et al. 2012. We used data from the Core Area for annual female survival (Table 5.1), and assumed male survival was 20% below female survival based on data presented in Zablan et al. (2003).

We did not test different scenarios for male survival since this parameter has little impact on population growth for polygynous species. Similar to percent breeding, we calculated SD due to environmental variation following Rohlf and Sokal (1981) and assumed demographic stochasticity was negligible. We assumed SD due to environmental variation was equal for males and female annual survival. For mate monopolization, we assumed 46% of males successfully sire offspring based on Bird et al. (2012).

We defined the population as sage-grouse within the Core Area and adjacent areas of South Dakota and Wyoming because collared hens demonstrated connectivity across political boundaries (see Chapter 6). We estimated initial population size to be 1,600 individuals based on an estimated 1,400 individuals in the Core Area (Montana) and adjacent areas in South Dakota (Taylor et al. 2010), which we conservatively increased by 200 individuals to account for population increases in 2013 (Fig. 1.3) and birds in adjacent areas of Wyoming. We used a conservative estimate for carrying capacity of 10,000 individuals. Lek data suggests that sage-grouse in the Core Area have approached 7,000 individuals, not including birds in adjacent areas of South Dakota and Wyoming (J. Ensign, FWP, unpublished).

Scenarios

Sage-grouse were subjected to extreme environmental conditions during the study (Appendix A), which impacted observed population vital rates. In particular, overwinter survival of hens was lowest during severe winter 2010–2011 (Chapter 4) and reproduction was lowest following flood conditions during spring 2011 (Chapters 2–3). We also suspect a minor WNv outbreak during late summer 2010 (Chapter 4). Therefore, we ran 2 basic scenarios during PVA analyses: 1) Normal: a scenario which censors decreased reproduction and survival associated with extreme weather events and the potential WNv outbreak, and probably provides the best estimate of population viability under normal to mild environmental conditions, and 2) Extreme: a pessimistic scenario that uses overall observed vital rates from the Core Area, including extreme weather periods and the potential WNv outbreak (Table 5.1). To more accurately incorporate the impacts of extreme weather and disease, we included them in population viability models as the following catastrophes: 1) severe winter: survival is

Table 5.1. Parameter estimates and SD due to environmental variance for Normal (data from severe weather events and a potential WNv outbreak censored) and Extreme (no data censored) scenarios.

	Scenario			
	Normal		Extreme	
Parameter	Estimate	SD	Estimate	SD
Percent breeding	53%	8%	50%	8%
Offspring/brood	7.3	1.6	7.1	1.6
Annual hen mortality	40%	2%	47%	8%

decreased by 15% during the winter season (Chapter 4), which equates to a 10% reduction in annual survival at a frequency of 3.3% (1 in 30 years), 2) flood: reproduction is decreased by 30% (calculated based on chicks produced per hen during flood year 2011 vs. 2010 and 2012; Table 3.3) at a frequency of 1% (1 in 100 years), and 3) mild WNv outbreak: survival is decreased by 15% during late summer (Chapter 4), which translates to a 10% reduction in annual survival at a frequency of 25% (1 in 4 years). To best evaluate population viability within the Core Area given available data, we ran a simulation for the Normal scenario plus all 3 catastrophes. To better understand the impact of each catastrophe, we ran the Normal scenario with each individually. To understand the contribution of major vital rates to population viability, we also ran scenarios where individual vital rates (percent breeding, chick survival, juvenile survival [birth to 1 year], and hen survival) were increased by 5%. These scenarios are useful to understand the impacts of factors such as habitat quality and predator densities. If we can predict the impact of these factors on population vital rates, PVA allows us to quantify the associated impact to population growth rates. We did not run scenarios including hunting harvest mortality because no radio-collared sage-grouse were harvested during the study (Chapter 4). We report the mean exponential population growth rate (r), associated SD, difference in r from the Normal scenario (Δ_r), probability of extinction (extinction definition: only one sex remaining), and mean time to extinction for each scenario.

RESULTS

Population viability results are summarized in Table 5.2. The Normal scenario with severe winter, flood and WNv catastrophes (the scenario that we chose to best approximate population viability for sage-grouse in the Core Area) has a growth rate (r) of -0.8%. The WNv catastrophe (Δ_r = -2.6%) had a greater impact on r than severe winter or flood catastrophes (≤ 0.4% reduction in r). Increasing vital rates by 5% resulted in $\Delta_r \geq +3.8\%$. Probability of extinction was 0% for all scenarios except the Extreme scenario, which had a 6% probability of extinction within 30 years and a mean time to extinction of 27 years.

Table 5.2. Mean stochastic exponential growth rate ($\bar{x}_r$), associated standard deviation (SD_r), difference in growth rate from the Normal scenario (Δ_r), probability of extinction within 30 years (PE), and mean time to extinction ($\bar{x}_{TE}$) in years for population viability analyses conducted in program VORTEX (Lacy et al. 2003). Tested scenarios included a base scenario for normal years (data from a severe winter, flood, and a suspected WNv outbreak censored) and extreme years (no data censored). We tested the Normal scenario with data from the severe winter, flood, and suspected WNv outbreak included as catastrophes, and also tested scenarios with 5% increases in hen survival (Hen ϕ^{+5}), chick survival (Chk ϕ^{+5}), juvenile (birth-1 year) survival (Juv ϕ^{+5}), and the percent of hens that successfully hatched at least one chick (%Breed^{+5}).

Scenario[1]	$\bar{x}_r$	SD_r	Δ_r	PE	$\bar{x}_{TE}$
Normal	+2.4%	0.183	0	0%	-
Normal +Severe Winter	+2.0%	0.184	-0.4%	0%	-
Normal +Flood	+2.2%	0.184	-0.2%	0%	-
Normal +WNv	-0.2%	0.189	-2.6%	0%	-
Normal + Severe Winter, Flood, WNv	-0.8%	0.191	-3.2%	0%	-
Normal: Hen ϕ^{+5}	+7.1%	0.173	+4.7%	0%	-
Normal: Chk ϕ^{+5}	+7.9%	0.179	+5.5%	0%	-
Normal: Juv ϕ^{+5}	+11.5%	0.178	+9.1%	0%	-
Normal: %Breed^{+5}	+6.2%	0.182	+3.8%	0%	-
Normal: Hen ϕ^{+5}, Juv ϕ^{+5}, %Breed^{+5}	+19.9%	0.169	+17.5%	0%	-
Extreme	-10.6%	0.288	-13.0%	6%	27

DISCUSSION

Population viability analyses should not be viewed as a crystal ball that can predict the future with certainty. Outcomes of individual iterations (which each represent potential real-world population trajectories) varied greatly due to random effects of environmental variation

and stochasticity. We also caution that data used to conduct this PVA was collected during a series of extreme years, which impacted rates of survival and reproduction. The Extreme scenario is certainly pessimistic because it considers data collected during extreme weather events as common occurrence. However, even though we incorporated observed effects of extreme weather into the Normal scenario as catastrophes, there were likely other, more indirect effects of abnormal weather that were impossible to quantify or censor. Therefore, vital rates used in the Normal scenario may be pessimistic (e.g., due to drought in 2012) or optimistic (e.g., because cover was good during all years of the study). Although PVA cannot predict the future with great certainty, it is a useful tool to better understand the likelihood of population persistence and factors driving population dynamics.

Overall PVA indicates that Core Area sage-grouse are very likely to persist at sustainable levels. The mean population growth rate for our most realistic scenario (Normal + Severe Winter, Flood, WNv; r = -0.8%) is indicative of an effectively stable population. Probability of extinction within 30 years was 0% for nearly every scenario. Even the pessimistic Extreme scenario had only a 6% probability of extinction in 30 years, and the mean time to extinction was 27 years. This indicates that even if Core Area populations were to decline as predicted by the Extreme scenario, local extinction is unlikely to be imminent. Severe weather impacted rates of survival and reproduction during the study. However, when the effects of severe weather were incorporated as catastrophes, they had little effect on population growth rates (≤ -0.4% reduction in r) because of their rarity.

We incorporated WNv as a catastrophe that would reduce late summer/fall survival by 15% based on reduced survival in the Core Area during 2010, which resulted in a 2.6% decrease in population growth rate. However, WNv mortality can be much more severe. Near-extirpation of local sage-grouse populations has been reported (e.g., 91% reduction in lek counts following WNv outbreak; Walker et al. 2004). On average, late summer/fall survival is reduced by 25% during WNv outbreaks, and population growth rates are reduced by 6–9% (Walker and Naugle 2011). Lacking that crystal ball, the future impact of WNv on sage-grouse in the Core Area is impossible to realistically quantify. Continued outbreaks similar to 2007 (Fig. 1.3) could severely reduce populations.

The potential for future WNv outbreaks is especially worrisome because PVA analysis indicates that, although the population is not undergoing a rapid decline, it is not undergoing rapid recovery since the 2007 outbreak. The Normal scenario with no catastrophes had a growth rate of only 2.4% annually, which is barely above stable. Another factor which was not considered in our PVA is future habitat loss, which can act synergistically with WNv to reduce populations (Taylor et al. 2010). However, PVA did indicate that increasing individual survival or reproduction parameters by 5% resulted in $\Delta_r \geq 3.8\%$. Simultaneously increasing juvenile survival, adult survival, and percent breeding resulted in $\Delta_r = 17.5\%$. This indicates the population has great potential to increase if environmental conditions, habitat conditions or other management actions improve survival and/or reproductive success. Reduced survival associated with repeated WNv outbreaks could hinder population persistence and recovery, especially if exacerbated by future habitat loss due to tillage or energy development. However, if current habitat conditions and mortality remain stable or improve, there is great potential for sage-grouse to continue to thrive and little potential for sage-grouse extinction in the Core Area.



- 6 -

Movements & Seasonal Habitat Use





INTRODUCTION

Sage-grouse exhibit a wide range of movement strategies, from using a single home range year-round to using multiple distinct seasonal ranges (Connelly et al. 2011*b*, Tack et al. 2011). Movements of up to 100 miles between seasonal ranges have been documented (Smith 2013). Sage-grouse seasonal movements may be driven by necessity (e.g. to access winter range in a fragmented landscape), but even within large expanses of prime habitat, sage-grouse may bypass suitable habitat to return to traditional ranges learned during their first year of life (Berry and Eng 1985, Connelly et al. 1988, Schroeder and Robb 2003).

Sage-grouse core areas in Montana were delineated based solely on lek locations and associated male counts (Chapter 1). Little was known about habitat use and movements of sage-grouse during the rest of their annual cycle. It was unknown if the Core Area (Fig. 1.2), as delineated, was adequate to meet the year-round needs of sage-grouse. Are sage-grouse observed on leks in the Core Area moving outside the boundaries of the Core Area to meet their seasonal needs? Should the boundary of the Core Area be adjusted to accommodate seasonal movements? Because important areas for sage-grouse are a function of both habitat and tradition (i.e., learned areas), tracking collared sage-grouse was necessary to understand sage-grouse use of the landscape.

Our objective was to quantify seasonal movements, site fidelity, and habitat use of sage-grouse within the Core Area to better understand how resident grouse use the landscape year-round and assess the adequacy of the Core Area, as delineated, to accommodate the life history needs of denizen grouse. The resulting information will help managers prioritize sage-grouse conservation efforts at a landscape level and compose sound recommendations to minimize the impacts of development and associated disturbance on resident sage-grouse.

METHODS

Our goal was to monitor radio-collared hens at least once per week from April–September and twice per month from October–March. Occasionally, hens were monitored less frequently due to severe weather events or logistical constraints. We used telemetry

techniques (Samuel and Fuller 1996) to locate hens on the ground from April–September. We conducted telemetry flights when hens could not be located on the ground and to locate all hens from October–March. At each location, we recorded status (e.g., live, nesting, brood-rearing), GPS location, habitat information, and other pertinent notes.

We recorded >2,800 unique locations for 94 radio-collared hens, thus it was not logistically feasible to exhaustively measure vegetation at each location. Therefore, we recorded basic habitat information to quantify seasonal habitat use. For ground and aerial locations, we classified habitat into 4 categories: sagebrush-steppe (≥1% shrub canopy cover), grassland (<1% shrub cover), alfalfa (including mixed grass/alfalfa hay fields), and wetland. For ground locations in sagebrush-steppe we visually estimated shrub canopy cover as 1–10%, 11–25%, or >25%, and estimated the average height of mature shrubs by taking a single height measurement of an average shrub. We also recorded whether a hen was located within 100 yards of a water source (e.g., pond, reservoir, creek or wetland) at all ground locations.

Analyses

We calculated the mean lek-to-nest distance and the percentage of hens that nested within 1, 2, 3, 4, and >4 mi from known leks in the Core Area. We selected these distances because other research has suggested sage-grouse tend to nest near leks (e.g., Braun et al. 1977) and the BLM commonly restricts activity within these distances to protect nesting grouse from various levels of disturbance. Female sage-grouse tend to make inter-lek movements during the breeding season (Dunn and Braun 1985), so we did not restrict analyses to the lek nearest a hen's capture location. However, this method may underestimate lek-to-nest distances because we did not confirm that hens visited the lek nearest to their nest location, nor was every lek surveyed every year to confirm activity. To better understand this bias, we calculated the distances between nests and leks known to be active during the study for a portion of the Core Area (the Draft Carter County Master Lease Plan [MLP] area; BLM 2013) that was exhaustively surveyed for leks each year. The MLP area comprises 29% of the Core Area.

To examine nesting-area fidelity, we calculated the median and range of distances between nests within a nesting season and among years for individual hens that nested more than once during the study. For brood hens, we calculated the mean and range of distances from nest locations to brood-rearing locations at 14 and 30 days post-hatch. Distances were calculated using Hawth's Tools (Beyer 2004) in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA).

We examined movements for each hen to determine if distinct seasonal ranges were used. We excluded data from hens that died before seasonal ranges could be established. An area was considered a distinct seasonal range if the hen was located in an area for several weeks with no overlapping locations during other seasons. We provide summaries of hen annual and seasonal movements, including number of seasonal ranges utilized, maximum length of seasonal ranges, distances moved between seasonal ranges, and the median date of movements between ranges. Distances (center to center) were calculated using the measure tool in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA).

We calculated minimum convex polygons (MCP) for hens that were tracked >1 year using Hawth's Tools. One hen that was tracked >1 year was excluded from MCP analysis because a malfunctioning radio collar resulted in large data gaps and a MCP that was biased small. Although MCPs are not accurate home-range size estimates (i.e. not all areas within an MCP are used by a hen), they provide a measure of how large of an area hens are using on the landscape. We include figures showing example movement patterns and MCPs. To assess the adequacy of the size of the Core Area to accommodate the life history needs of resident grouse, we present figures showing the overall dispersion of study hens during spring–fall (March 1–October 28) and winter (November 1–February 28) overlaid with core and connectivity area delineations from South Dakota (South Dakota Game, Fish, and Parks unpublished draft sage-grouse core area delineations obtained December 2013) and Wyoming (Wyoming Game and Fish Department 2010).

To better understand the influence of winter severity on sage-grouse movements, we calculated the average distance moved between each within-winter telemetry survey and total point-to-point distances moved by year using hens as sampling units. It was necessary to

calculate both of these metrics because the number of winter telemetry flights varied among years, which confounds comparison of movements among winters. Higher survey frequency would be expected to increase total distance moved but decrease the average distance moved between consecutive within-winter telemetry surveys. For 30 hens that were tracked >1 winter, we examined fidelity to winter range and calculated the average distance between winter ranges when different wintering areas were used.

To examine seasonal habitat use, we compiled data on habitat variables for each hen for 4 seasons: breeding (March 1–April 15), nesting/brood-rearing (April 16–July 15), late summer/fall (July 16–October 31), and winter (November 1–February 28). We further divided the nesting/brood-rearing season based on a hen's status into prenesting, nesting, early brood-rearing (hatch–30 days post-hatch), late brood-rearing (>30 days post-hatch), and broodless hens (for hens who did not initiate nests or following nest or brood failure). We treated hens as sampling units and calculated averages for each habitat variable for each season/status.

RESULTS

Movements

The average distance between sage-grouse nests and known leks was 1.15 miles (SE = 0.13 miles). Fifty-nine percent (90/152) of nests were within one mile of a lek, 84% (127/152) within 2 miles, 93% (142/152) within 3 miles, and 97% (147/152) within 4 miles. All nests were within 5.0 miles of a lek. When analyses were restricted to known-active leks in the MLP area, 47% (25/53) of nests were within one mile of a known active lek, 68% (36/53) were within 2 miles, 88% (46/53) were within 3 miles, and 92% (49/53) were within 4 miles. All nests were within 4.6 miles of an active lek in the MLP. Hens generally exhibited nesting area fidelity; the overall median distance between nests was 0.28 mi (Table 6.1). The overall range of between-year nest distances was much larger for yearlings than adults (Table 6.1). Hens moved an average of 0.53 mile from nests in the first 14 days post-hatch, and 0.68 mile 30 days post-hatch. The maximum distance traveled from the nest by a brooding hen in the first 30 days was 3.17 miles (Table 6.2).

Table 6.1. Within-year, between-year, and overall distance among nests for 16 yearling and 34 adult sage-grouse hens in the Southeast Montana Sage-Grouse Core Area that nested more than once during the study.

	Within-year		Between-year		Overall	
	Median (mi)	Range (mi)	Median (mi)	Range (mi)	Median (mi)	Range (mi)
Yearling	0.46	0.04–3.42	0.36	0.11–14.74	0.34	0.06–14.74
Adult	0.45	0.11–3.88	0.25	0.04–2.18	0.25	0.04–2.77
Both	0.46	0.04–3.88	0.28	0.04–14.74	0.28	0.04–14.74

Table 6.2. Distances between nest and brooding sites for sage-grouse hens 14 and 30 days post-hatch in southeastern Montana, 2010–2012.

	14 days post hatch				30 days post hatch		
	n	x̄ (mi)	SE (mi)	Range (mi)	x̄ (mi)	SE (mi)	Range (mi)
Year							
2010	18	0.55	0.10	0.11–1.61	0.66	0.11	0.16–1.55
2011	12	0.52	0.11	0.02–1.04	0.68	0.12	0.05–1.55
2012	10	0.49	0.10	0.24–1.17	0.81	0.27	0.13–3.17
Age							
Adult	27	0.53	0.07	0.11–1.61	0.75	0.12	0.05–3.17
Yearling	13	0.52	0.12	0.02–1.43	0.68	0.12	0.16–1.55
Overall	40	0.53	0.06	0.02–1.61	0.68	0.09	0.05–3.17

Seasonal movement patterns varied widely among individual sage-grouse hens (Fig. 6.1). Of 40 hens that were followed for a minimum of one year, 17.5% (7/40) used one area throughout their annual cycle, while 65% (26/40) used 2 seasonal ranges, and 17.5% (7/40) used 3 seasonal ranges. Of 53 hens that were followed from nesting to fall, 7% (2/28) of hens that successfully raised a brood moved between distinct nesting and late summer seasonal ranges, compared to 24% (6/25) of broodless hens. For hens with a single home range, the average maximum length of MCPs was 7.5 mi (n = 7, range 4.0–22.0 mi). The maximum length of nesting/brood-rearing and summer/fall MCPs (n = 57, $\bar{x}$ = 2.1 mi, range 0.3–6.8 mi) tended to be smaller than the maximum length of winter MCPs (n = 38, $\bar{x}$ = 5.8 mi, range 1.4–24.0 mi). The average distance between nesting and late summer seasonal ranges was 6.8 mi (range 4.0–14.3 mi). The average distance traveled to winter ranges was 10.7 mi (n = 31; range 3.6–33.0

mi). The median date of movements from either a summer or fall range to a winter range was October 15 (range September 10–November 15), and the median date of movements from winter ranges to nesting/summer ranges was March 20 (range March 12–June 3). The average minimum convex polygon size for hens that were tracked ≥1 year was 71.2 mi^2 (SE = 8.8 mi^2, range 7.9–238.1 mi^2; see Fig. 6.2 for examples). The overall dispersion of radio-collared hens during the breeding through fall seasons (March 1 to October 31) and winter (November 1–February 28) are pictured in Figures 6.3 and 6.4.

The average distance moved between telemetry surveys and total distance moved over winter were greater during winters 2009–10 and 2010–11 than milder 2011–12 or 2012–13 winters (Table 6.3). Fifty-four percent (12/22) of hens used a different winter range during the extreme 2010–11 winter than either the previous or following winters (Table 6.4). Four of these hens used a single home range year-round except during the severe winter. In comparison, only 18% (3/17) of hens used a different winter range during the mild 2011–12 winter compared with the average 2012–13 winter. The average distance between winter range for 15 hens that used different areas between years was 8.6 miles (SE = 1.1 mi, range = 3.6–17.5 mi). Many of the hens that used a different range during the severe winter moved there after beginning winter from the same winter range used during milder winters.

Seasonal Habitat Use

Seasonal habitat use is summarized in Table 6.5. More than 98% of sage-grouse locations during breeding, prenesting, nesting, and winter were in sagebrush-steppe habitat, compared to 79–83% of locations during brood-rearing. Sage-grouse tended to use dense stands of sagebrush (>25% canopy cover) in the greatest proportion during prenesting and nesting, and moderate density sagebrush (11–25% canopy cover) in the greatest proportion during winter and breeding. Sage-grouse tended to be located adjacent to water sources or wetlands most often during the late brood-rearing period.

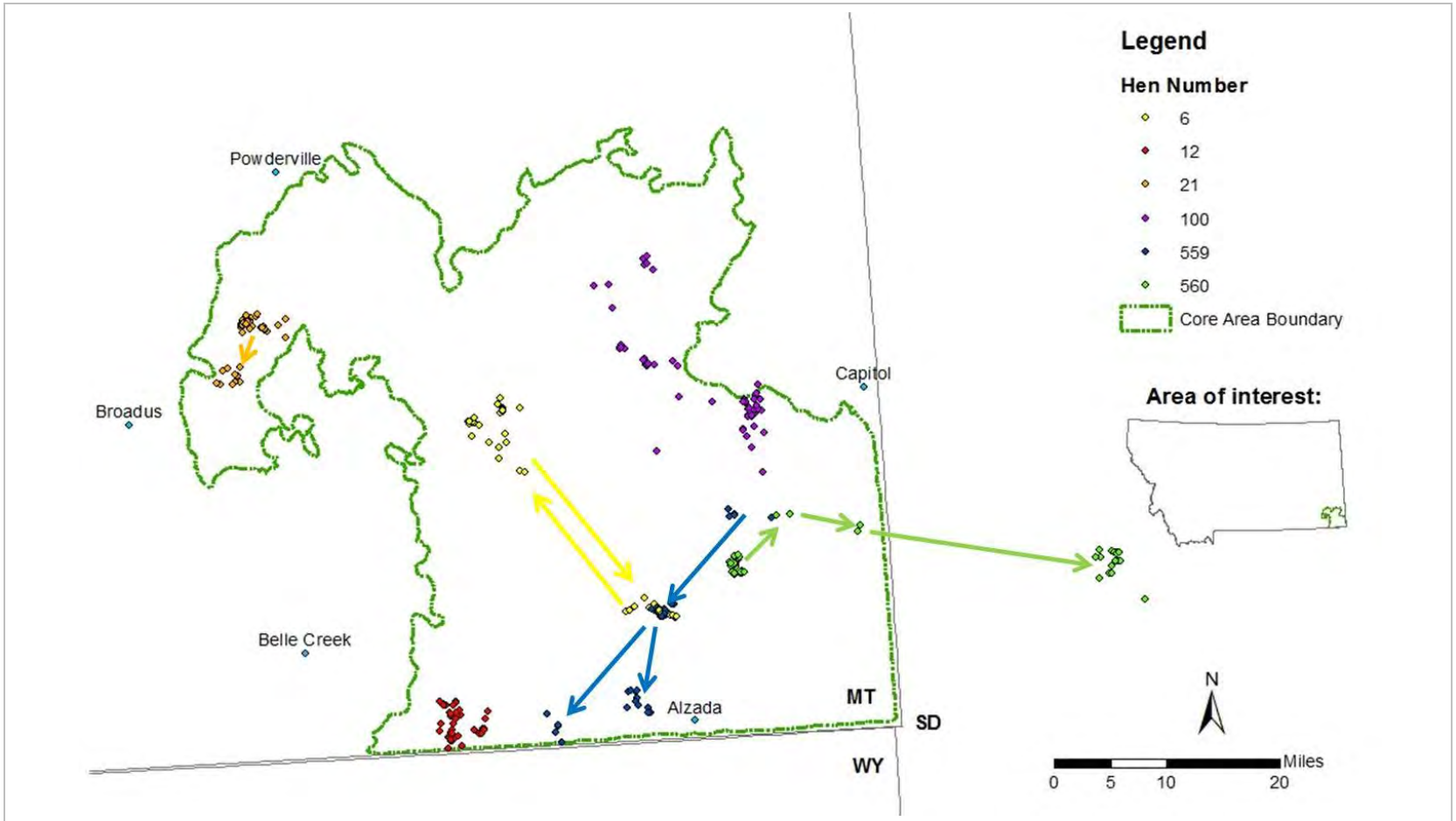


Figure 6.1. Example movement patterns of radio-collared sage-grouse hens in southeastern Montana. Hen 21 (orange) used one area from nesting through fall, then traveled southwest to a distinct winter range. Hen 6 (yellow) used one area during breeding, nesting, and early brood-rearing, then traveled southeast to a late summer range but returned northwest for winter. Hen 100 (purple) used a large area (maximum length: 22 miles) throughout the year but did not establish distinct seasonal ranges. Hen 12 (red) used a single, small home range year-round (maximum length: 4.5 miles). Hen 559 (blue) was a 3-stage migrant that used distinct breeding, nesting–fall, and winter ranges. Hen 559 (blue) altered her winter range during the severe 2010–11 winter, but nested and summered in the same range every year. Hen 560 (green) used one range during nesting–fall, then traveled more than 40 miles east to winter, including stopovers.

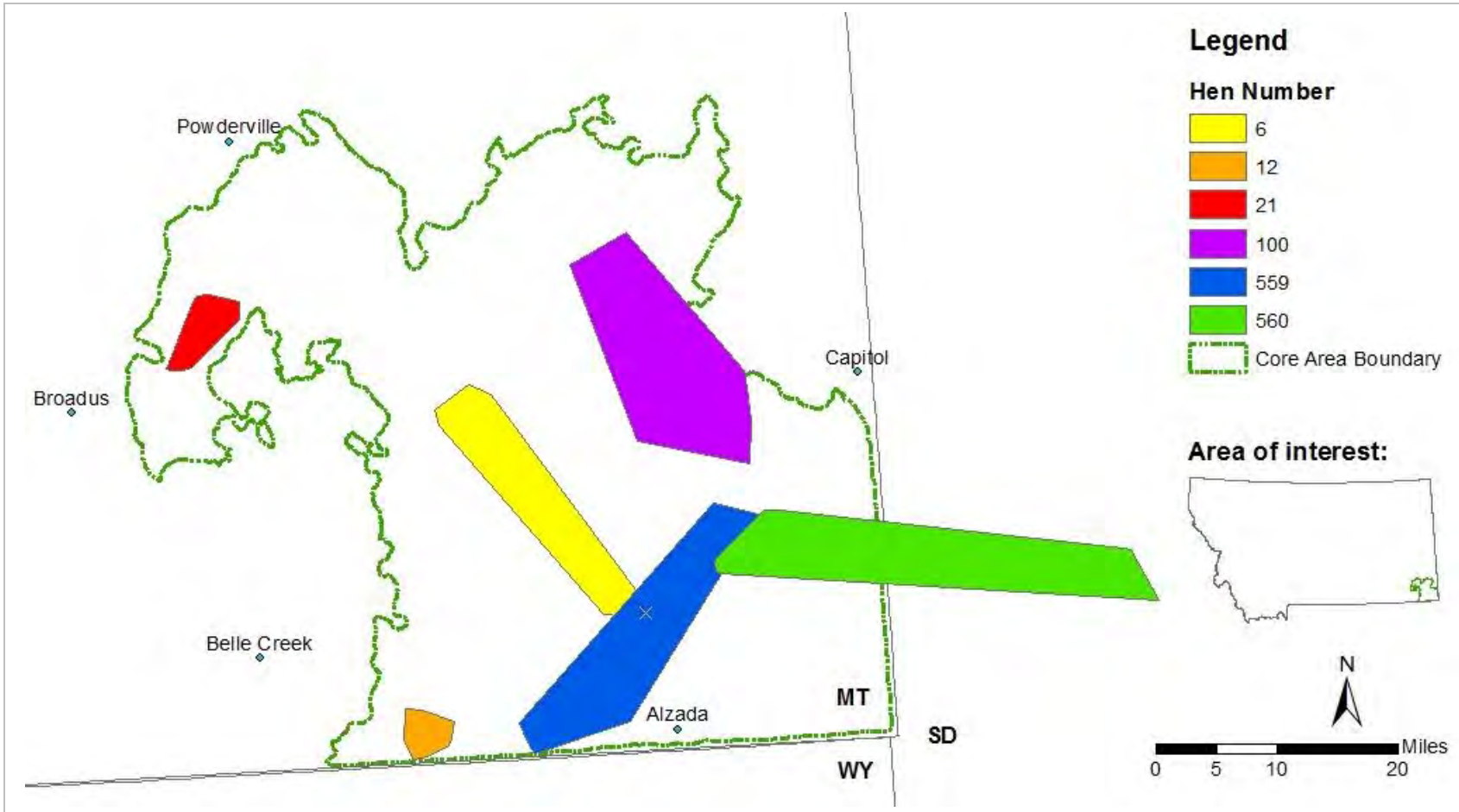


Figure 6.2. Example minimum convex polygons for radio-collared sage-grouse hens provide a feel for how large of an area individual sage-grouse used on the landscape.

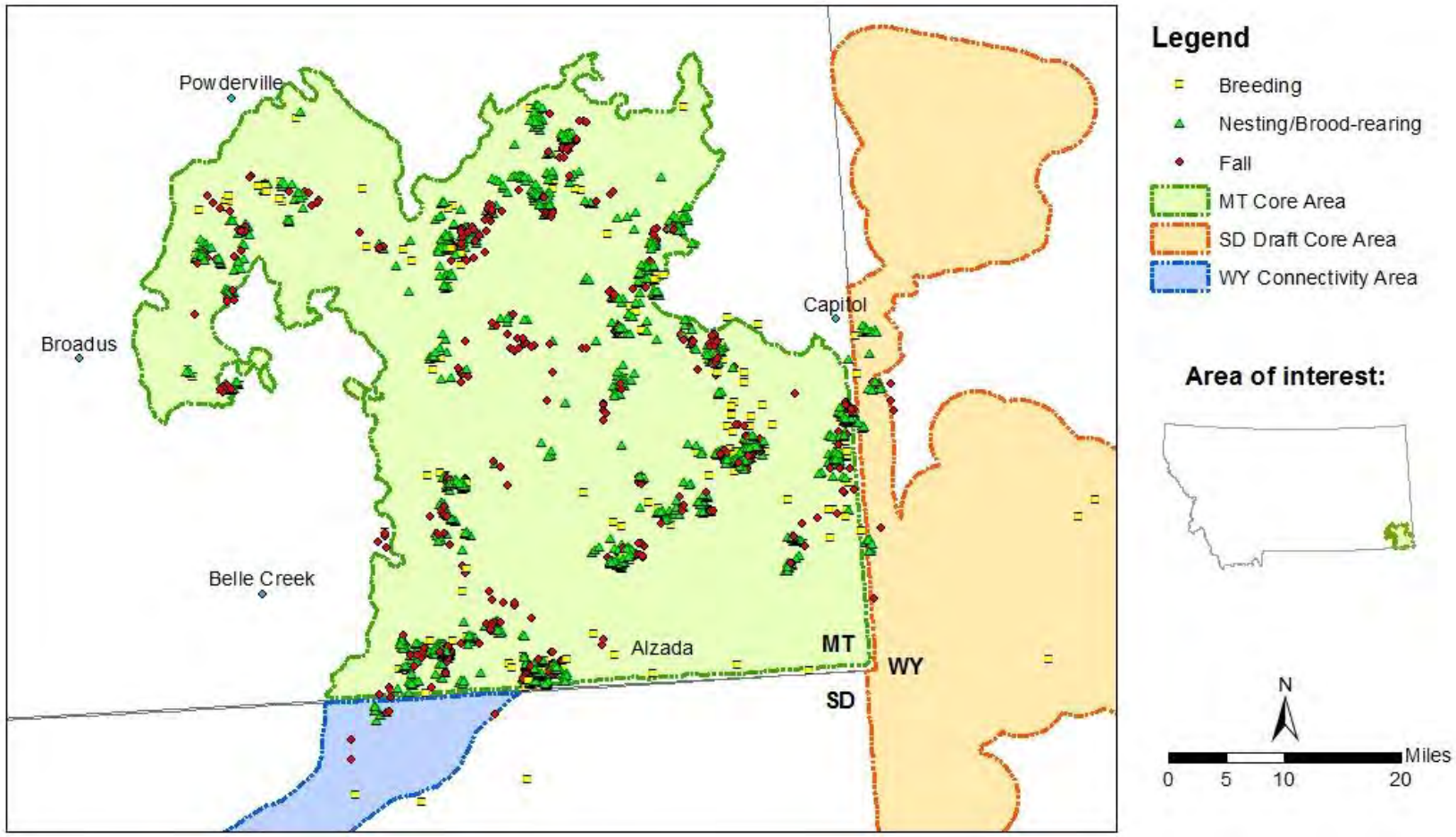


Figure 6.3. Overall dispersion of radio-collared sage-grouse during the breeding (March 1–April 15), nesting/brood-rearing (April 16–July 15), and late summer/fall (July 16–October 31) seasons.

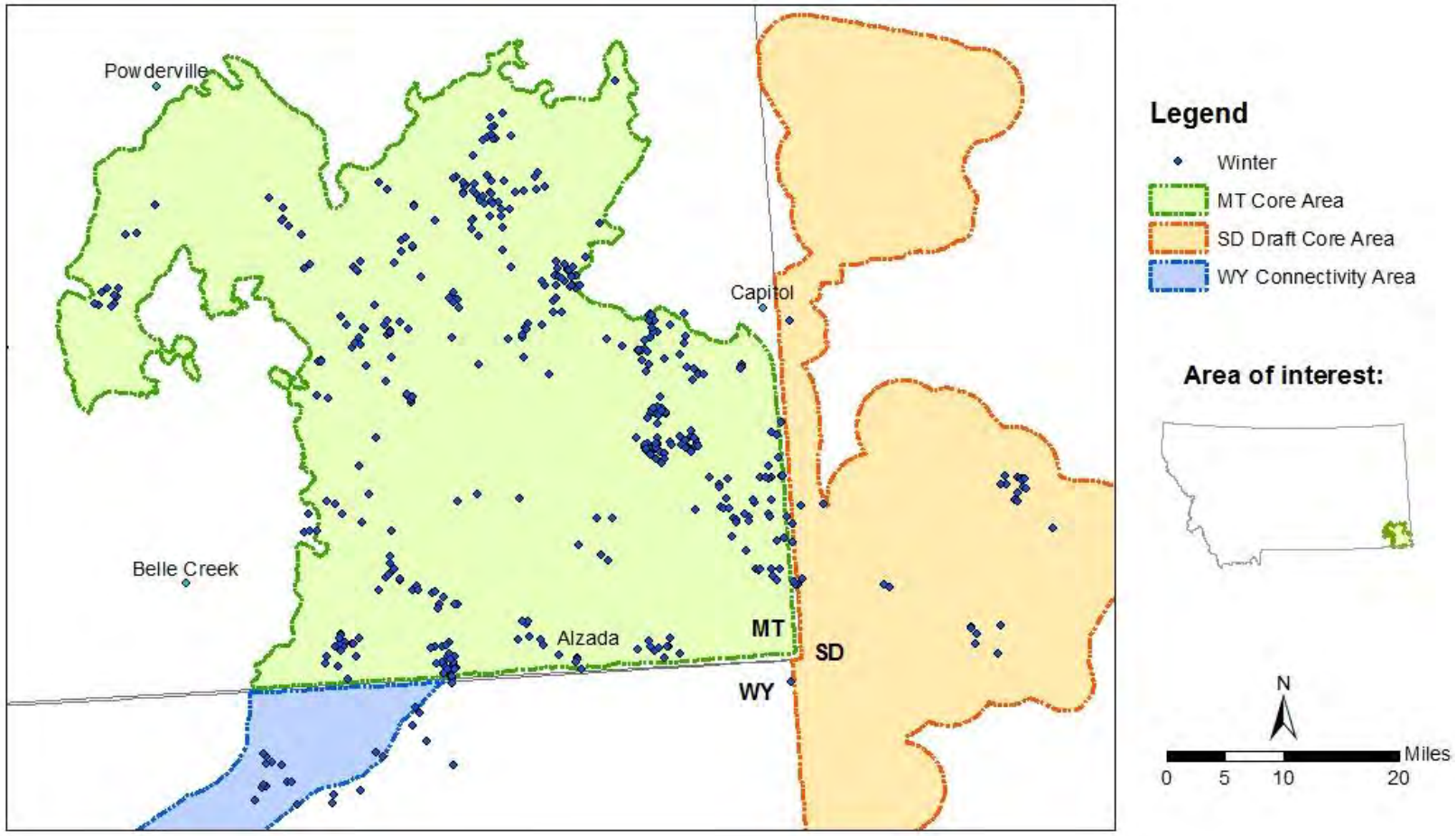


Figure 6.4. Overall dispersion of radio-collared sage-grouse during winter (November 1–February 28).

Table 6.3. Average distance moved between telemetry surveys ($\bar{x}$ mi/survey) and total distance moved over winter (November 1–February 28) for radio-marked sage-grouse hens in southeast Montana. Total distance was calculated by summing distances between consecutive survey locations.

					Total Distance		
Winter	Severity	# Hens[A]	# Surveys[B,C]	$\bar{x}$ mi/survey	$\bar{x}$ (mi)	SE (mi)	Range (mi)
2009–10	Tough	6	7	2.7	19.2	2.8	5.5–24.2
2010–11	Severe	25	7	2.5	17.5	1.4	7.8–35.4
2011–12	Mild	29	6	1.9	11.6	1.6	3.9–49.1
2012–13	Average	12	5	1.8	9.1	1.2	4.5–17.6

[A] The number of hens that were tracked and survived the entire winter
[B] The number of aerial telemetry surveys conducted from November 1 - February 28
[C] Unequal sample sizes among winters confound comparison of movements among winters. Higher survey frequency would be expected to increase total distance moved but decrease the average distance moved between consecutive within-winter telemetry surveys.

Table 6.4. Fidelity to winter range for 30 sage-grouse hens that were radio tracked more than one winter. Twenty-two hens were tracked 2 winters, 7 for 3 winters, and one for 4 winters, for a total of 39 hen-winters. The average distance between winter range for 15 hens than used different areas between years was 8.6 miles (SE = 1.1 mi).

Years	Winter Severity	# Hens	# Different[A]	% Different[A]
2009–10 vs. 2010–11	Tough vs. Severe	5	3	60%
2010–11 vs. 2011–12	Severe vs. Mild	17	9	53%
2011–12 vs. 2012–13	Mild vs. Average	17	3	18%

[A] The number and percent of hens that used different wintering areas between years.

DISCUSSION

Mean distance between nests and the nearest lek was 1.15 miles, which is at the low end of the range reported in other studies (0.8–3.2 mi; reviewed in Connelly et al. 2011*a*). That distance was slightly larger when only known active leks were analyzed in the MLP area ($\bar{x}$ =1.55 mi). Lek-to-nest distances tend to be higher in developed or fragmented (e.g., by tillage) than intact habitat (reviewed in Connelly et. al. 2011*a*). Therefore, relatively low lek-to-nest distances in the Core Area likely reflect low levels of fragmentation and relatively intact sagebrush-steppe habitats on the landscape.

Table 6.5. Habitat use for radio-collared sage-grouse in southeastern Montana by season and reproductive status. The percent of locations in each habitat type and separated by sagebrush canopy coverage, average height of mature shrubs for locations in shrub-steppe habitat, and the percent of locations within 100 yards of a water source (e.g., pond, reservoir creek) or wetland ($Water_{100}$).

			Habitat Type[B]									
						Sagebrush-steppe				Shrub Ht[C]		
Season/Status[A]	Hens	Locations	Grass	Alfalfa	Wetland	1–10%	11–25%	>25%	Total	x̄	SE	$Water_{100}$
Breeding	58	108	2%	0%	0%	28%	63%	7%	98%	13.5	1.21	0%
Prenesting	79	339	2%	0%	0%	30%	42%	26%	98%	13.4	2.37	23%
Nesting	73	144	0%	0%	0%	26%	45%	28%	100%	15.5	3.58	18%
Early brood-rearing	40	209	16%	1%	1%	43%*	31%	8%	83%*	13.3	1.86	16%
Late brood-rearing	34	196	15%	3%	3%	29%*	40%	10%	79%*	18.1	3.38	40%
Broodless	48	494	12%	1%	1%	31%	44%	11%	86%	15.2	2.91	25%
Late summer/fall	57	497	6%	2%	2%	26%	55%	10%	90%	13.9	3.57	11%
Winter	48	471	0%	0%	0%	15%	78%	7%	100%	NC	NC	NC

[A] Seasons = Breeding (March 1–April 15), nesting/brood-rearing (April 16–July 15), late summer/fall (July 16–October 31), and winter (November 1–February 28). Status: we divided the nesting/brood-rearing season into prenesting, nesting, early brood-rearing (hatch–30 days post-hatch), late brood-rearing (>30 days post-hatch), and nonbreeding (for hens who did not initiate nests or following nest or brood failure).

[B] Grass = grassland (<1% shrub canopy cover; including native/introduced range and grass hay fields), Alfalfa = alfalfa or mixed grass/alfalfa hayfield, Wetland = wetlands or mesic areas, Sagebrush-steppe by canopy coverage and total locations in sagebrush-steppe habitat.

[C] NC = Not collected because sage-grouse were located aerially during winter.

*Includes 2% of locations where greasewood is the dominant shrub.

Restriction radii surrounding leks for surface disturbing activities typically range from 1.0–4.0 mi, and 59% of nests were within one mile of a known lek location, 84% within 2 miles, 93% within 3 miles, and 97% within 4 miles. These percentages were lower when only known active leks were considered: only 47% of nests were found within one mile of a lek, but the majority (92%) of nests were still found within 4 miles of an active lek. Nest success exerts great influence on population growth rates for sage-grouse. Therefore, a one-mile buffer is inadequate to avoid significant population impacts associated with development activities. We recommend a minimum 4 mile buffer for highly-intrusive practices within suitable sagebrush habitat. Brood hens tended to stay close to nest sites for the first 30 days following hatch ($\bar{x}$ = 0.68 mi), and thus restrictive radii placed around leks to protect nesting habitat may also benefit young broods.

Sage-grouse exhibited strong nest site fidelity. The median distance between nests and renests (0.46 mi) and the median distance between consecutive-year nests (0.28 mi) were lower than reported in other studies (1.2–1.6 mi between nests and renests, 0.4–1.9 mi between consecutive-year nests; reviewed *in* Connelly et al. 2011*a*). Median distances between nests were only slightly larger for yearlings (0.34 mi) than adults (0.25 mi), which indicates that nesting sage-grouse often exhibit fidelity to their first nesting location. However, the maximum distance between nests was much larger for yearlings (14.74 mi) than adults (3.88 mi), which indicates that young hens may, in some cases, exhibit considerable plasticity with regard to nesting locations.

Brood hens moved an average 0.68 mile during the first 30 days post hatch, which is similar to movements reported in other studies ($\bar{x}$ = 0.49–0.93 mi; reviewed *in* Connelly et al. 2011*a*). Movements during the first 14 days post-hatch were similar among years ($\bar{x}$ = 0.53 mi, maximum = 1.61 mi), but the average and maximum distance moved by 30 days post-hatch was greater in drought year 2012 ($\bar{x}$ = 0.81, max = 3.2 mi) than other years ($\bar{x}$ < 0.68 mi, max = 1.6 mi). This suggests that brood movements are limited by chick motility during the first 14 days post-hatch (Schroeder et al. 1999), but that by 30 days post-hatch hens may move broods longer distances to find higher quality foraging habitat during dry years.

As summer progressed and vegetation in uplands desiccated, both brood and broodless hens tended to move to more mesic areas, and used non-sagebrush habitats (e.g., grasslands, wetlands, alfalfa fields) in greater proportion, which has been well-documented in sage-grouse (Klebenow 1969, Martin 1970, Peterson 1970, Wallestad 1971). Interestingly, brood hens were less likely to move to distinct late summer ranges (7%; 2/28) than broodless hens (6/25; 24%), which would suggest that chicks may continue to have limited motility during late summer. However, late brooding hens were found more often in non-sagebrush mesic habitats than broodless hens, which suggests that high-quality brood-rearing habitat was available for brood hens in close proximity to nesting/early brood-rearing locations. We suspect that late summer movements by broodless hens may be driven by other factors (e.g., that hens may be searching for other broodless hens to flock with), or that the trend for broodless hens to be more likely to use distinct late summer ranges may be an artifact of small sample size.

Sage-grouse are sagebrush obligates that depend on sagebrush for food and cover throughout their annual cycle (Patterson 1952, Dalke et al. 1963). More than 79% of locations in any season, and >98% of locations during breeding, prenesting, nesting, and winter were in sagebrush-steppe habitat, similar to sage-grouse elsewhere (Connelly et al. 2011*c*). Sage-grouse tended to use dense stands sagebrush (>25% canopy cover) in the greatest proportion during prenesting and nesting, and moderate density sagebrush (11–25% canopy cover) in the greatest proportion during winter and breeding. This moderate to dense sagebrush is oftentimes what people think of when they visualize sage-grouse habitat, yet sage-grouse frequently (>25% of locations) used areas with sparse (1–10% canopy cover) sagebrush during spring through fall. Even during winter, 15% of locations were sagebrush with <10% canopy cover. Observed patterns of habitat use in the Core Area likely reflect habitat availability for a population on the eastern edge of the range, but nevertheless highlight the importance of heterogeneous (including areas with dense, moderate, and sparse canopy cover) sagebrush habitat to resident sage-grouse.

Movement patterns for individual sage-grouse hens varied greatly in the Core Area. A majority (60%) of hens tracked >1 year made movements >6.2 miles, often used as the definition of a migratory population (Connelly et al. 2000*b*). Yet, roughly 18% made no

movements at all between seasonal ranges, and many traveled <6.2 miles between ranges. Fifty-four percent of hens utilized different winter ranges and movement patterns during the severe 2010–11 winter compared with previous or subsequent winters, and 4 hens were non-migratory except during the severe winter. Variation in migratory strategies within populations has been documented for sage-grouse (e.g., Swanson 2009, Fedy et al. 2012), as has plasticity related to severe winter events (Smith 2013).

The majority of locations of collared sage-grouse fell within the boundary of the Core Area in Montana, but many hens made movements into areas of South Dakota and Wyoming adjacent to the Core Area. Similarly, Swanson (2009) documented movements of radio-collared sage-grouse between South Dakota and the Core Area. Cooperation among states will be necessary to maintain sagebrush habitat on the landscape and manage this sage-grouse population across state borders. Sage-grouse core/connectivity areas provide excellent framework to cooperatively manage sage-grouse populations across administrative boundaries. South Dakota draft core areas encompassed nearly all locations from radio-collared sage-grouse hens. However, core area boundaries for Montana and South Dakota do not match up near the historic town of Capitol, Montana. Locations of collared sage-grouse in the area, including a handful of locations between the 2 core areas, suggest the area is important from a connectivity standpoint. Therefore, we recommend that the Montana Core Area be expanded to include suitable sagebrush habitat south of the Little Missouri River and Hackberry Creek. For hens that moved into adjacent areas of Wyoming, the majority of locations were within a connectivity area, but many locations were outside of the connectivity area to the east, including important and critical winter range (Fig. 7.1). We recommend the Wyoming connectivity area be expanded to incorporate sage-grouse winter range delineated in Figure 7.1. Similarly, 3 winter range polygons (Fig. 7.1) extended <1.75 miles outside of the Core Area in Montana and should be included in the Core Area delineation.



- 7 -

Winter Use & Vegetation



INTRODUCTION

A critical component of sage-grouse year-round habitat, winter range can exert strong influence on sage-grouse distributions and persistence (Aldridge and Boyce 2007, Connelly et al. 2011*c*). Sage-grouse populations can be severely impacted by degradation, fragmentation or loss of winter habitat (Doherty et al. 2008). Winter habitat characteristics vary among populations of sage-grouse (Connelly et al. 2000*b*). Sage-grouse typically use only a percentage of available sagebrush habitat during winter, and may travel long distances to winter range (Beck 1977, Connelly et al. 2011*c*, Smith 2013). Therefore, identifying population-specific winter use areas and winter habitat characteristics is extremely important. Winter 2010–11 was among the most severe on record, and winter 2011–12 was among the mildest on record (Appendix A). The contrast between these 2 winters provided unique data to 1) delineate winter use areas and classify them as critical, important, or general winter range, and 2) to quantify and compare winter habitat characteristics based on winter severity and winter range importance. The resulting information will improve our understanding of the requirements of wintering sage-grouse within the Core Area (Fig. 1.2) to inform land-use planning. It also provides valuable site-specific baseline data for comparison with other studies and the Core Area in the future.

METHODS

Delineating winter use areas

We conducted aerial telemetry flights to locate radio-collared hens 1–2 times monthly October–March. We marked winter use locations using a handheld GPS unit, opportunistically recorded flock sizes, and visually estimated snow depth. We delineated winter-use areas using locations from radio-collared grouse supplemented with data from the FWP sage-grouse winter database (SGWD; 99 locations within the Core Area), which contains observations of wintering grouse or tracks obtained during aerial surveys conducted during 2002 and 2006–10. First, we created fixed kernel density estimates (1,094-yd bandwidth) of all sage-grouse winter (November 1–February 28) locations using Hawth's Tools (Beyer 2004) in ArcGIS 9.3

(Environmental Systems Research Institute, Redlands, CA), and used the 90% volume contour as the basis for polygons. We then added locations from the FWP SGWD, and adjusted polygons to include these locations if they were nearby (≤0.5 mi). In one case, a polygon consisted entirely of SGWD locations. We subjectively designated polygons into 3 categories based on the following criteria:

- **Critical winter range** consistently wintered large (≥50) flocks of sage-grouse. Many were used by several radio-marked hens that joined together and hens often localized in these polygons for the entire winter. Many contained points from the SGWD in addition to locations from radio marked hens. They were used during periods of deep snow (≥12") and during the severe 2010–11 winter.
- **Important winter range** consistently wintered medium sized (<50) flocks of sage-grouse. Similar to critical winter range, important winter range polygons often were used by multiple radio marked hens, were used for most of the winter, often overlapped locations from the SGWD, and were used during periods of deep snow and during the severe 2010–11 winter.
- **General winter range** contains only a few winter locations. Flock sizes were small (<20) or unknown. These areas are either minor wintering grounds or require more data to characterize their importance.

We did not present isolated winter use locations from radio marked hens if they occurred early in the winter or during mild winters, and had flock sizes <5 or unknown. Similarly, we did not map isolated SGWD locations for small flocks, but did map isolated locations where >20 sage-grouse were observed, because these may represent important sage-grouse wintering grounds. We present the total area of critical, important, and general winter range, and the percent of the Core Area that we designated as winter range.

Winter vegetation

We randomly chose a minimum of 3 aerial winter locations for each radio-collared hen from each from winter, for a total of 237 locations. We measured vegetation at winter use

locations during summer 2012, and assumed that shrub characteristics did not change during the study. Winter telemetry locations were marked using handheld GPS from fixed-wing aircraft and were often based solely on telemetry fixes rather than visual locations (birds were not usually flushed), thus points were considered accurate to the general area. Therefore, points were occasionally located in areas that did not include sagebrush cover on the 55-yd transect but sagebrush stands existed nearby (<100 yards). In those cases, we randomly selected a location within the sagebrush stand because our goal was to quantify characteristics of sagebrush stands in sage-grouse winter range, and we knew that grouse had wintered in the general area. We centered 55-yd line transects oriented north-south at each location. We measured the height of the nearest sagebrush at each meter along the transect, and calculated shrub density and canopy cover using the same methods described in the nesting vegetation section. We also measured distances from these locations to trees and human structures (e.g. roads, fences, etc.).

We summarized sagebrush characteristics by year and tested for differences between the severe 2010–11 and mild 2011–12 winter using *t*-tests. We did not test winter 2009–10 due to low sample size. We also tested for differences in sagebrush characteristics between critical and important winter range areas using *t*-tests (general winter range was not tested due to low sample size). We used a χ^2 test for independence to test for differences in slope between 2010–11 and 2011–12 and between critical and important winter range. For locations with >5% slope, we created a rose diagram to summarize aspects. We provide the percent of locations and summary statistics for locations that were within 0.25 miles of trees and human structures. All statistical tests were performed at $\alpha = 0.05$.

RESULTS

Delineating winter use areas

We delineated 48 sage-grouse winter use polygons (Fig. 7.1), with a total of 246.4 mi^2 designated as critical (13 polygons), 186.6 mi^2 designated as important (23 polygons), and 39.7

mi^2 designated as general sage-grouse winter range (12 polygons). In total, 472.8 mi^2 were designated as winter range: 396.4 mi^2 within the Core Area in Montana (19% of the total 2101 mi^2 Core Area) and the remainder in Wyoming and South Dakota.

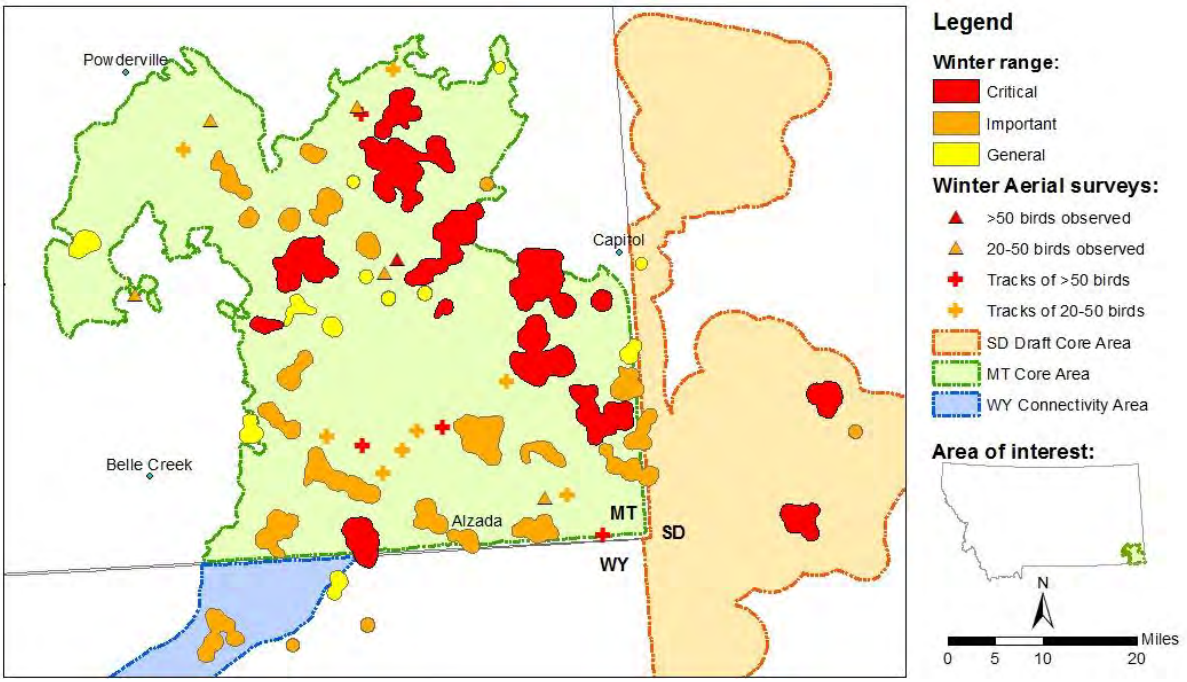


Figure 7.1. Critical (red), important (orange), and general (yellow) sage-grouse winter range polygons in southeastern Montana and adjacent areas of Wyoming and South Dakota. Isolated aerial survey locations from the FWP sage-grouse winter database were mapped where birds or tracks indicated flocks of ≥20 sage-grouse.

Winter Vegetation

Sagebrush was taller at 2010–11 winter locations than 2011–12 winter locations (t_{207} = 3.95, P < 0.001; Table 7.1), but sagebrush canopy cover (t_{207} = 0.41, P = 0.68) and sagebrush density (t_{207} = 1.63, P = 0.10) did not differ between winters. Critical winter areas had lower sagebrush height (t_{122} = 4.57, P = <0.001) and higher shrub density (t_{192} = 2.29, P = 0.02) than important winter areas (Table 7.1). Percent sagebrush cover did not differ between critical and important winter areas (t_{204} = 0.54, P = 0.59). Example winter locations are shown in Figure 7.2.

Table 7.1. Sagebrush canopy cover, density, and average height at sage-grouse winter locations in southeast Montana by year and winter range type.

		Canopy Cover (%)			Density (shrubs/yd^2)			Sagebrush Height (in)		
	n	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Year										
2009–2010	25	15	1.6	0–30	1.2	0.18	0.0–3.4	9.3	1.0	5.4–23.3
2010–2011	108	11	0.7	1–29	0.9	0.05	0.1–2.8	10.2	0.4	4.2–31.5
2011–2012	104	11	0.7	0–31	1.0	0.06	0.03–3.1	7.9	0.4	3.4–27.3
Winter Range										
Critical	132	11	0.6	0–29	1.1	0.06	0.0–3.4	7.8	0.3	3.4–23.0
Important	75	12	0.9	1–31	0.9	0.06	0.1–2.0	10.6	0.5	4.2–27.3
General	17	13	1.7	1–23	0.8	0.13	0.1–1.8	10.7	1.3	4.1–23.4
All Locations	237	11	0.5	0–31	1.0	0.04	0.0–3.4	9.1	0.7	3.4–27.3

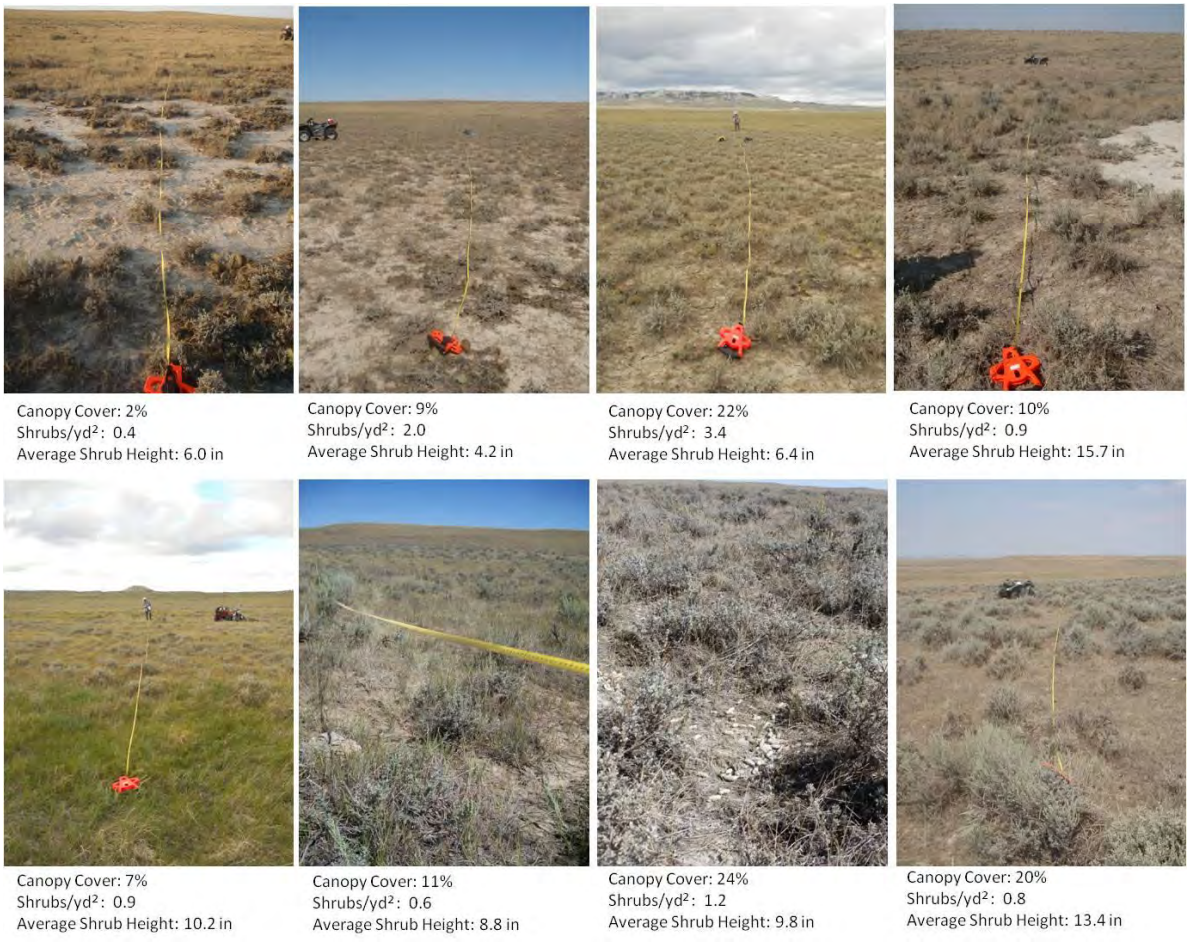


Figure 7.2. Example sage-grouse winter locations in the Southeast Montana Sage-Grouse Core Area.

Locations in critical winter range polygons had lower slopes than locations in important winter range polygons (χ^2 = 29.9, df = 2, P < 0.001; Table 7.2). Slope at winter use locations did not differ among years (χ^2 = 2.4, df = 2, P =0.29; Table 7.2). The majority (89%) of locations had <5% slope, and the maximum slope was 20%. Locations with slopes >5% were distributed mostly between north, south, and west aspects (Fig. 7.3).

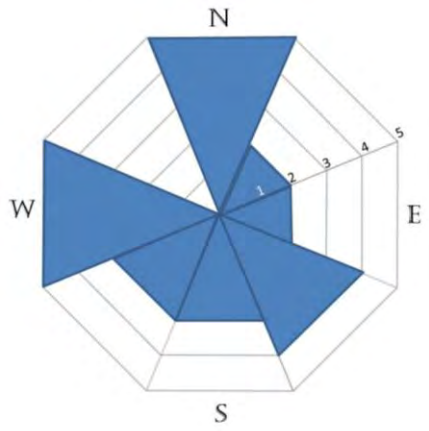


Figure 7.3. Rose diagram showing the aspects for 28 sage-grouse winter locations with slope >5%. Most (89%) locations had slopes ≤5%

Fifty-eight percent of sage-grouse winter locations were within 0.25 miles from a fence, road, or other human structure (Table 7.3). Thirty-eight percent of locations were near fences, and more than a third of locations were within 0.25 miles of roads (ranging from pickup trails to

Table 7.2. Slope was lower in critical versus important sage-grouse winter range polygons (χ^2 = 29.9, df = 2, P < 0.001).

		Slope		
Winter Range	*n*	0%	1–5%	>5%
Critical	132	51%	45%	4%
Important	75	19%	59%	23%
All Locations	237	38%	51%	11%

Table 7.3. Percent of sage-grouse winter locations that were within 0.25 miles from fences, roads, trees, powerlines, buildings/other structures, or trees, and the mean, SE, and range of distances measured (within 0.25 mi) to each. Percentages do not sum to 100 because some locations were near more than one item and 38% of locations did not have human structures or trees within 0.25 miles.

Distance to	%	$\bar{x}$ (yd)	SE (yd)	Range (yd)
Fence	38% (91/237)	199	13.2	21–492
Road	34% (81/237)	163	13.9	1–492
Powerline	4% (9/237)	166	34.8	50– 390
Building/Other Structure	4% (9/237)	177	30.2	66–328
Tree	13% (30/237)	203	27.6	1–470

highways). Thirteen percent of locations were near trees, typically sparsely-treed creek bottoms. Few (≤4%) locations were within 0.25 miles from power lines, buildings, or other human structures.

DISCUSSION

We designated 19% of the Core Area as sage-grouse winter range. We recommend the Wyoming connectivity area be expanded to incorporate sage-grouse winter range delineated in Figure 7.1. Similarly, 3 winter range polygons (Fig. 7.1) extended <1.75 miles outside of the Core Area in Montana and should be included in the Core Area delineation.

The winter use polygons we present provide a strong foundation that land managers can use to guide management and minimize impacts of development on sage-grouse in the Core Area. However, the polygons should be viewed as a work-in-progress. As more data becomes available it may be justified to refine or expand existing polygons, or identify additional areas as critical or important winter range.

In particular, we were only able to follow one hen from the northeastern portion of the Core Area. This hen was tracked during mild winters 2011–12 and 2012–13, and remained in the Core Area throughout winter. Note the single general winter range (yellow) polygon northeast of Broadus, MT (Fig. 7.4). Based upon sagebrush habitat availability, it is likely that other sage-grouse winter use areas exist in the Core Area south of Powderville, MT. Several wintering grounds were identified northwest of Powderville, MT during aerial surveys. We speculate that sage-grouse from the Core Area might winter in these areas, but more information is needed. We recommend these wintering areas be given similar protection and consideration as sage-grouse core areas until more information can be gathered.

Critical sage-grouse winter range was characterized by gentler topography, shorter shrubs, and greater shrub density than important or general winter range. Similarly, winter use locations in North and South Dakota were characterized by shorter, denser sagebrush than random locations (Swanson et al. 2013). These results are contrary to many studies, where sage-grouse select areas with taller shrubs because sagebrush exposed above snow is necessary

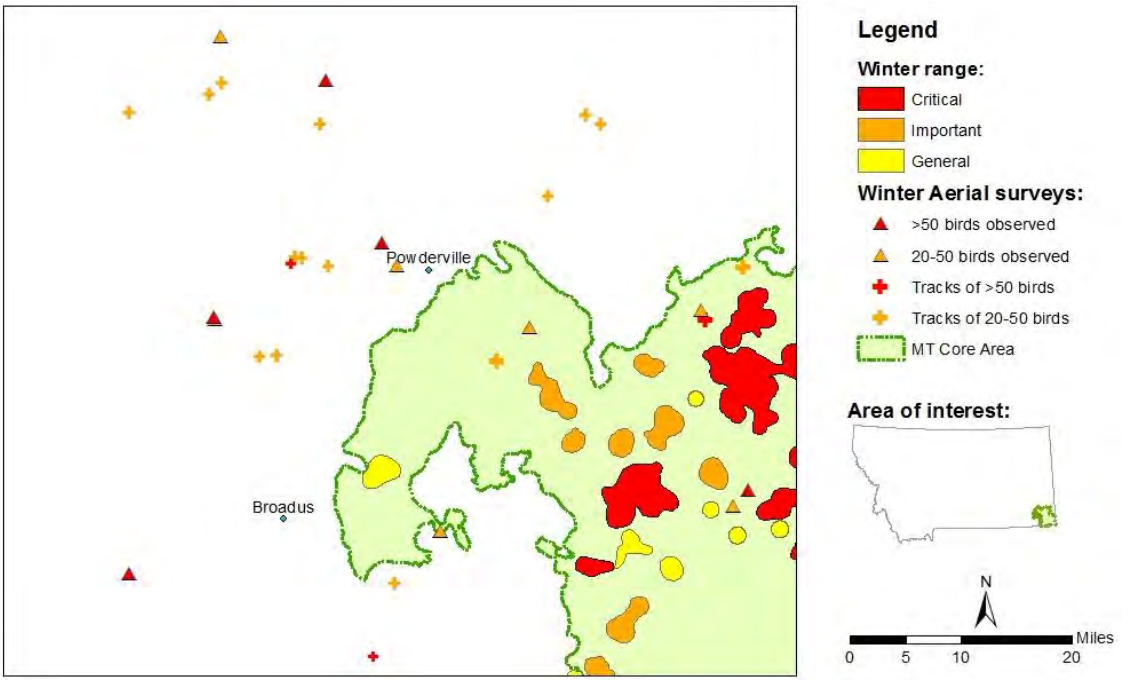


Figure 7.4. Winter use data was scarce for hens from the extreme northeast finger of the Core Area due to hen mortalities. It is likely that other, unidentified, winter use areas exist in Core Area south of Powderville, MT. Additionally, several wintering grounds were identified northwest of Powderville, MT during aerial surveys. Sage-grouse from the Core Area might winter in these areas, but more information is needed.

cover and forage (e.g., Patterson 1952, Robertson 1991, Connelly et al. 2000*b*). Overall, sagebrush canopy cover ($\bar{x}$ = 11%) and height ($\bar{x}$ = 9.1 in) were similar to averages reported from comparable habitat in North and South Dakota (canopy cover 15%, height 7.9 in; Swanson et al. 2013), but at the low end of the range reported by studies elsewhere ($\bar{x}$ canopy cover = 12–43%, $\bar{x}$ height = 8–22 in; reviewed *in* Connelly et al. 2000*b*). The overall average sagebrush height was less than the 10–14 inches of sagebrush above snow levels recommended by Connelly et al. (2000*b*). Lower-than-average sagebrush canopy cover and height at winter use locations in the Core Area and the Dakotas is probably an artifact of sage-grouse near the eastern edge of their range and a reflection of the availability of suitable sagebrush winter habitat (Swanson et al. 2013). The apparent preference for shorter sagebrush heights may reflect low average snowfall (November–February snowfall averages 6.6 in/month; Table A.3) in the Core Area. In most years, flats with short, dense shrub cover probably remain windswept and open, providing access to sagebrush throughout winter.

Winter 2010–11 was extreme, and snow buried stands of sagebrush throughout much of the Core Area (Fig. 4.2, Appendix A). As a result, 54% of hens shifted their winter ranges (Chapter 6). Sagebrush at winter use locations during the severe 2010–11 winter was taller ($\bar{x}$ = 10.2 in) than during the mild 2011–12 winter ($\bar{x}$ = 7.9 in). However, we do not suggest that sagebrush height within winter ranges is a limiting factor for sage-grouse in the Core Area for 3 reasons: 1) Sage-grouse did not necessarily use the tallest or densest sagebrush available. Even during severe winters, average shrub canopy cover (11%), density (0.9 shrubs/yd^2) and height (10.2 in) were lower than nesting locations which averaged 16% canopy cover, 0.98 shrubs/yd^2, and 12.2 in shrub height (Chapter 2). 2) Sagebrush height interacts with topography to determine sagebrush availability. Taller sagebrush may result in greater snow drift making food and cover less available to wintering grouse than windswept areas with shorter sagebrush. 3) Although survival during winter 2010–11 (83%) was lower than other years (≥95%; Table 4.2), and observations of grouse roosting on a barren snowscape suggested habitat was limiting during that year (Fig 4.2), a winter that extreme is a rare event (expected frequency: 1 in 30 years; Appendix A) and has little impact on long-term population growth rates (Δ_r = -0.004; Table 5.2).



- 8 -

Management Implications





Sage-grouse Core Areas comprise <10% of Montana's land area yet support more than half of the sage-grouse in the state (NRCS 2010). They are vitally important to the long term conservation and sustainability of sage-grouse. The Southeastern Montana Sage-grouse Core Area (Fig. 1.2; hereafter: Core Area) is particularly important because it provides connectivity with sage-grouse populations in adjacent states and represents a stronghold for sage-grouse near the eastern edge of their range. Population viability analyses (PVA) suggest that sage-grouse will continue to persist at sustainable levels in the Core Area unless catastrophic events (e.g., disease outbreaks) occur and provided the quality and extent of sage-grouse habitat in the Core Area is maintained or improved (Chapter 5).

Traditional family-owned ranching operations, the predominant local stakeholders in the Core Area, have historically managed land in a manner that is compatible with sage-grouse conservation: they have maintained intact sagebrush grasslands. Maintaining this traditional land use by working with local stakeholders to implement conservation efforts is the most important management action we can do to ensure the future of sage-grouse in the Core Area. While ranchers must run profitable operations, they also have a vested interest in the long-term sustainability of land use practices and are well-poised to collaborate with wildlife and range professionals to maintain and improve sage-grouse habitat.

To maximize the effectiveness of conservation efforts, stakeholders should consider organizing planning efforts on a landscape level following the model outlined by Neudecker et al. (2011) for community-based landscape conservation. This model involves developing private-public land partnerships that simultaneously benefit local communities, wildlife, and other natural resources. Under the model, conservation efforts are implemented at the local scale (e.g., individual ranches), but planning efforts consider the landscape as a whole. We recommend the following to maintain and enhance sage-grouse habitat in the Core Area:

Maintain Large Expanses of Intact Sagebrush Habitat

Sage-grouse are sagebrush obligates that depend on sagebrush for winter forage (>95% of winter diet) and year-round cover (Patterson 1952, Dalke et al. 1963, Remington and Braun 1985). Loss, fragmentation and degradation of sagebrush habitat are primary threats to sage-

grouse rangewide (USFWS 2010). Future energy development in the Core Area is of concern, since numerous studies have highlighted the deleterious effects of energy development on sage-grouse populations (reviewed *in* Naugle et al. 2011). For example, at well densities >1 well per square mile, lek losses of 32–77% were documented in Wyoming, which is 2–5 times greater than losses observed in undeveloped areas (Doherty et al. 2010). The Core Area currently contains large areas of unfragmented sagebrush-steppe habitat (Montana Sage Grouse Work Group 2005, Taylor et al. 2010). Therefore, management within the Core Area should, first and foremost, prioritize maintaining existing sagebrush-steppe habitat by minimizing habitat loss, fragmentation, and degradation due to factors such as tillage, industrial development, fire, and herbicide.

Management of sagebrush habitat

When people visualize sage-grouse habitat, they typically think of vast landscapes filled with tall, dense sagebrush. However, the Core Area is located at the eastern edge of the range of Wyoming big sagebrush, and is characterized by smaller, less dense sagebrush than elsewhere in the sage-grouse range. Sage-grouse in the study used sagebrush-steppe habitat extensively throughout their annual cycle (92% of locations), but frequently (27% of locations) used areas with sparse (1–10%) sagebrush canopy cover (Table 6.5). Dense sagebrush (>25% canopy cover) was used in the greatest proportion during nesting, and moderate density sagebrush (11–25% canopy cover) was used in the greatest proportion during winter (Table 6.5). Observed patterns of habitat use in the Core Area likely reflect habitat availability on the eastern edge of their range, but nevertheless highlight the importance of maintaining heterogeneous (including areas with thick, moderate, and sparse canopy cover) sagebrush habitat. Given that sagebrush characteristics may be intrinsically limited by local soil and climactic conditions, management guidelines that emphasize certain heights or densities of sagebrush may be unachievable within the Core Area.

Occasionally, sage-grouse management guidelines recommend sagebrush reduction to promote forb production for brood-rearing. This practice is not recommended for areas where forb production is limited by rainfall (Kirol et al. 2012). Forb production and richness in the

Core Area were strongly influenced by spring and summer precipitation. Forbs comprised 15% horizontal cover at early brood-rearing sites during wet years 2010 and 2011 but less than 5% during drought year 2012, and forb species richness at brood-rearing locations was highest during a year of extreme precipitation (2011) and lowest during drought (2012; Table 3.6). Reducing sagebrush cover would not be expected to improve forb production.

Survival of hens during severe winter 2010–11 (83%) was about 15% lower than winters 2011–12 and 2012–13 (95 and 100%), and sagebrush at winter use locations during 2010–11 winter was taller ($\bar{x}$ = 10.2 in) than during the mild 2011–12 winter ($\bar{x}$ = 7.9 in). However, we do not suggest that sagebrush height within winter ranges is a limiting factor for sage-grouse in the Core Area for 3 reasons: 1) sage-grouse did not necessarily use the tallest or thickest sagebrush available. 2) Sagebrush height coupled with topography determined sagebrush availability. Taller sagebrush may result in greater snow drift making food and cover less available to wintering grouse than windswept areas with shorter sagebrush. 3) Extreme winters are rare (expected frequency: 1 in 30 years; Appendix A) and have little impact on long-term population growth rates (Δ_r = -0.004; Table 5.2). Management of wintering sage-grouse habitat should focus on protecting the integrity of winter use areas rather than sagebrush manipulation.

Utilize Livestock Grazing as a Management Tool

We observed no negative impacts of livestock on nesting or brood-rearing grouse. Twenty-seven percent of nests were in pastures with livestock concurrently present, no nests were destroyed due to trampling, and apparent nest success was higher for nests in pastures with livestock (59%) than pastures without livestock (38%). Further, vegetation structure did not limit nest success (Table 2.5), which suggests that grazing did not limit nest success by reducing nest cover. Similar to nests, 47% of brood locations were in pastures with livestock concurrently present and brood success from 0–14 days post-hatch was higher for broods hatched in pastures with livestock (79%) than without (61%). Grazed pastures may be attractive to brood hens because cattle in large summer pastures do not typically consume vegetation uniformly, which results in a heterogeneous mix of open grazed areas where chicks can forage interspersed with ungrazed or lightly grazed areas that provide escape cover. The

mechanism driving higher nest and brood success in pastures with livestock is unknown; it may be a result of predators avoiding livestock or predators selecting areas with more homogeneous cover (Kirby and Grosz 1995). It may also reflect predator control efforts in areas with livestock. Overall, results from our study concur with research elsewhere that managed grazing is compatible with sage-grouse conservation, but we caution that we did not rigorously quantify the complex interrelationships among grazing, vegetation, and sage-grouse nest and brood success. We also caution that the study occurred during years with abundant live and/or residual cover (Figs. 2.2 and 3.3). Grazing practices in the Core Area might impact sage-grouse during periods of prolonged (>1 year) drought, when both live and residual cover are limited.

Even during years of abundant live or residual cover, there is always potential for improved grazing management. We recommend producers utilize rotational grazing systems consisting of large pastures that incorporate rest during the growing season and rotate season of use. Resting pastures benefits livestock and producers by improving rangeland health and productivity, and also benefits sage-grouse by providing areas with dense hiding cover. Periods of rest allow plants to build root systems and carbohydrate reserves, resulting in plants that are more robust and productive. Resting pastures maximizes seed production and allows seedling establishment to take place. This is especially important for preferred forage species that, when given a choice, livestock consume first. These preferred species must be given reprieve from grazing and allowed opportunities to reproduce. Finally, rest allows residual organic material to accumulate between plants, which enriches and builds soil, while reducing both wind and water erosion (McCarthy 2003). Rotating the season of use further promotes plant diversity and ensures a variety of vegetation states, including areas with dense cover, exist on the landscape at any given time.

Although periods of rest can benefit rangeland, livestock, and sage-grouse, we do not recommend rest from grazing altogether. Rangelands evolved with grazing, and grazing remains an integral part of grassland systems that provides periodic disturbance necessary to maintain ecosystem productivity. Grazing action is important to dislodge ripe seeds which are sown into the soil by trampling, thus improving seedling establishment (McCarthy 2003). Grazing removes residual growth and returns organic material to the soil, which improves the

soil, makes plants more palatable, and improves forage quality. Managed grazing can result in increased forb cover and diversity, and secondarily increased insect availability, which can benefit sage-grouse chicks (Beck and Mitchell 2000, Huwer et al. 2008, Rebholz 2007). For example, greater consumption of forbs and insects resulted in higher long-term productivity of sage-grouse compared to areas with lower availability of preferred food sources where chicks consumed primarily sagebrush (Drut et al. 1994*b*). Managed grazing may be particularly important in dry climates where forb availability limits chick survival (Aldridge and Brigham 2002) and few tools exist for managers to increase forb cover (Fischer et al. 1996).

Working with producers to maintain and improve grazing practices may be important to boost populations of sage-grouse in the Core Area because PVA indicated that, although the local sage-grouse population is not undergoing drastic declines, nor is it undergoing rapid recovery following a 2007 outbreak of WNv (Chapter 5). The benefits of managed grazing—improved cover and forage—can improve all population vital rates. Improved nutrition can increase egg production, nesting attempts, chick survival, and overwinter survival. Improved cover can benefit survival of nests, broods, juvenile, and adult sage-grouse. Population viability analyses indicated there is high potential for Core Area sage-grouse populations to increase, especially if management actions that simultaneously benefit survival and reproductive success, such as managed grazing, are implemented on a landscape scale. Population viability scenarios where juvenile survival, adult survival, and percent breeding were simultaneously increased by 5% resulted in a 17.5% increase in population growth rate (Table 5.2). However, grazing management will only benefit Core Area sage-grouse if existing large expanses of sagebrush are maintained, because the benefits of grass structure to population vital rates are secondary to landscape integrity (Taylor et al. 2010).

Predator Control vs. Habitat Management

Although the majority of sage-grouse mortalities and nest failures were due to predation, we do not recommend predator control for several reasons. First, population vital rates observed in the study were normal for sage-grouse and we expected the majority of mortalities and nest failures to be a result of predation. Sage-grouse do not typically die of old

age, and nest predation is a fact of life for all ground nesting birds. Ground nesting birds have evolved successful life history strategies to deal with nest predation (e.g., high fecundity, high population turnover, ability to renest, and great biotic potential for populations to increase during favorable conditions). Second, the bulk of mortality was attributed to avian predation. All raptors are federally-protected under the 1918 Migratory Bird Treaty Act, and eagles are further protected under the 1940 Bald and Golden Eagle Protection Act. Controlling avian predators is not possible under our current regulatory framework. Third, predator control often has unintended consequences. For example, lethal control of coyotes may allow for an increase the abundance of mesopredators (e.g., red fox, striped skunk) which are more adept at preying on sage-grouse hens and nests (Mezquida et al. 2006). Most broadband lethal predator control substances (e.g., sodium fluoroacetate [1080]) are banned by federal law. Fourth, predator control programs designed for game bird conservation have resulted in short term increases in postbreeding populations, but long term breeding numbers remain unaffected in high quality habitat (Côté and Sutherland 1997, Baines et al. 2004). Finally, predator control is expensive and only effective in the short term in small areas with intense control of all predators (Connelly et al. 2000*a*, Schroeder and Baydack 2001). In contrast, managing habitat provides long-term, wider-range benefits for survival (Schroeder and Baydack 2001). Vegetation management which promotes live and residual herbaceous cover can provide good visual and olfactory cover from predators and also increases population productivity by improving nest and brood success (Delong et al. 1995, Connelly et al. 2004, Coates and Delehanty 2010). Managing for extensive patches of suitable habitat can result in lower nest density, making it harder for predators to locate nests, thereby increasing nest success. Moreover, managing for abundant herbaceous cover provides nutritional benefits for sage-grouse which may further improve survival and production (Connelly et al. 2004, Gregg et al. 2006, Huwer et al. 2008).

Implement Conservation Efforts on a Landscape Scale

Sage-grouse require large, intact expanses of sagebrush in order to thrive (Connelly et al. 2011*c*). The Core Area boundary in Montana contained nearly every location from radio-

marked hens in the state, which provides evidence that the core area approach (i.e., delineating priority areas for sage-grouse conservation based on lek densities) has great potential to benefit sage-grouse. However, many hens made movements into South Dakota and Wyoming adjacent to the Core Area, and cooperation among states will be necessary to maintain this sage-grouse population. The core area approach also provides an excellent framework to cooperatively manage sage-grouse populations across administrative boundaries. We recommend minor adjustments to the Montana Core Area and Wyoming connectivity area to create a cohesive boundary and incorporate winter range (see Chapters 6–7). The South Dakota draft core area encompassed nearly all locations from radio-collared sage-grouse hens.

Landscape-level conservation of sage-grouse will require organization and cooperation of various stakeholders. The Core Area is a mix of private (54%), BLM (36%) and state (10%) surface ownership. The BLM has outlined practices to conserve sage-grouse in their draft Resource Management Plan, and Montana's Greater Sage-grouse Habitat Conservation Advisory Council (2013) has outlined practices to conserve sage-grouse habitat with regulatory authority on state lands and for activities that require a permit from the State of Montana (this document is currently in draft form and undergoing review by the governor). A variety of programs such as the Sage Grouse Initiative (www.sagegrouseinitiative.com), the FWP Upland Game Bird Habitat Enhancement Program (http://fwp.mt.gov/fishAndWildlife/habitat/wildlife/programs/uplandgamebird/habitat.html), and Habitat Montana (http://fwp.mt.gov/mtoutdoors/ HTML/articles/2004/HabitatMontana.htm) can assist private landowners interested in sage-grouse conservation and help organize conservation efforts on a larger scale. Ideally, conservation planning would extend to general sage-grouse habitat outside of the Core Area, since these areas are important for connectivity with populations elsewhere in and adjacent to Montana.

When Projects Must Occur, Plan to Minimize the Impacts

Development and other landscape altering projects within the Core Area should be approached with caution and forethought, considering the immediate, long term and cumulative impacts of such actions. Do alternatives exist which would make the project

unnecessary? Can the project be conducted outside of core sage-grouse habitat? When projects must occur within the Core Area, they should be carefully planned to minimize the impacts on resident grouse. Is it possible to conduct the project adjacent to existing development, thereby minimizing habitat fragmentation? How can the footprint of the project be minimized? Can the project occur within patches of unsuitable sage-grouse habitat? What other steps can be taken to minimize impacts to sage-grouse? Consideration of sage-grouse needs early in the planning process will help avoid and minimize impacts to resident sage-grouse as well as other species. Project-specific recommendations are beyond the scope of this paper. At a minimum, we recommend special consideration be given surrounding sage-grouse leks and winter range. The recommendations below may be adapted and modified based on site and project specifics. For example, we recommend a 4 mile buffer around leks for highly intrusive practices but if within the 4 mile buffer unsuitable sage-grouse habitat exists, it may be reasonable to allow development to occur in those areas. Potential impacts to sage-grouse should be evaluated on a site-specific, case-by-case, project-by-project basis.

Breeding, nesting, and brood-rearing

Restriction radii surrounding leks typically range from 1.0–4.0 mi. Fifty-nine percent of nests were within one mile of a known lek location, 84% within 2 miles, 93% within 3 miles, and 97% within 4 miles. Additionally, chicks have limited mobility (weak flight occurs at approximately 10 days post-hatch, strong flight at 5 weeks of age; Schroeder et al. 1999) and brood hens tended to stay close to nest sites for the first 30 days following hatch ($\bar{x}$ = 0.68 mi). Thus restrictive radii placed around leks may also benefit young broods, which is important because most chick mortality occurs within the first 4 weeks after hatching (Gregg et al. 2007, Dahlgren et al. 2010*a*), and chick survival is one of the most important parameters influencing population growth rates for sage-grouse (Taylor et al. 2010). Therefore, a one-mile buffer is inadequate to avoid significant population impacts associated with development activities. We recommend a minimum 4 mile buffer for highly-intrusive practices.

For activities that will result in habitat destruction, we recommend no surface occupancy (NSO) in all sagebrush-steppe habitat within the Core Area, and especially within the

above-listed radii. When projects will cause disturbance (e.g., noise) but have no long-term impact to habitat, timing restrictions may be sufficient to protect breeding, nesting, and brood-rearing sage-grouse. Timing restrictions often run from March 1–June 15, but many hens remain on nests and the bulk of the early brood-rearing season occurs after June 15. Therefore, we recommend timing restrictions be maintained until July 15. In most years nearly all nesting would be complete, all but the latest-hatched chicks would be >2 weeks old, and more than half of broods would have reached 30 days by July 15. Land managers may consider extending timing restrictions even further during wet years or years with a protracted nesting season.

Winter Range

We designated 19% of the Core Area as sage-grouse winter range (Fig. 7.1). We recommend NSO for activities that will result in habitat degradation, or timing restrictions from December 1 to March 31 for activities that will have no long-term impacts to habitat, within critical and important wintering areas. We recommend additional aerial surveys be conducted within and surrounding general winter range where data is limited, since it may be necessary to expand these areas or further classify them as important or critical winter range. We also recommend additional aerial winter surveys in and adjacent to the northeastern portion of the Core Area, since winter data from radio-collared hens was limited in that area (Fig. 7.4). Pending further data, it would be prudent to consider known winter-use areas outside the Core Area (Fig. 7.4) as potentially important wintering areas for Core Area sage-grouse and apply NSO and timing restrictions as appropriate.

Minimize West Nile Virus Outbreaks

Mortality due to WNv can result in significant local population declines (e.g., Walker et al. 2007). On average, late summer/fall survival is reduced by 25% during WNv outbreaks, and population growth rates are reduced by 6–9% (Walker and Naugle 2011). An outbreak in 2007 severely reduced sage-grouse numbers in the Core Area (Fig. 1.3). The future impact of WNv on sage-grouse in the Core Area is impossible to realistically quantify, but WNv outbreaks are a

major concern because population viability analyses indicated that, although the Core Area population is not undergoing a rapid decline at present, it also has not recovered from the 2007 WNv outbreak.

Few tools exist to reduce WNv outbreaks other than eliminating mosquito breeding habitat (i.e., standing water; Zou et al. 2006, Walker and Naugle 2011). We recommend, whenever possible, producers interested in creating new water developments for livestock utilize wells and pipelines rather than stock dams. Management of existing water impoundments should focus on maintaining wetland functionality because fully-functional wetlands contain predators including amphibians, insects, birds, and fish that eat mosquito larvae (USEPA 2004). Maintaining large landscapes of intact sagebrush may also be important to minimize the impacts of WNv since habitat loss acts synergistically with WNv to reduce populations (Taylor et al. 2010).

– Acknowledgements –

We are indebted to the numerous private landowners that provided access to sage-grouse habitat on their land. The project would not have been possible without local support. In particular, we thank the Bischoff family and Arbuckle Ranch for providing field housing. Dedicated field technicians Ashley Beyer, Chris Binschus, Lindsey Bischoff, Kaitlin Haidle, Darin Newton, Jackie Tooke, and numerous other volunteers made the project a success despite challenging field conditions. Darin Newton also assisted with database management and data analyses. Dean Waltee offered his expertise and assistance on the project from start to finish. Kent Undlin provided guidance on the project and valuable editorial comments. We are grateful to Neil Cadwell, Chad Cyrus, Monte Reder, and Erland Laird for piloting telemetry and survey flights. Capture and handling protocols were approved by the state of Montana Institutional Animal Care and Use Committee.

– Literature Cited –

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for greater sage-grouse. Ecological Applications 17:508-526.

Aldridge, C. L., and M. B. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433-444.

Baines, D., R. Moss, and D. Dugan. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. Journal of Applied Ecology 41:59-71.

Barker, W. T., K. K. Sedivec, T. A. Messmer, K. F. Higgins, and D. R. Hertel. 1990. Effects of specialized grazing systems on waterfowl production in south central North Dakota. US Fish and Wildlife Service Publication.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47:114-118.

Beck, T. D. 1977. Sage Grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18-26.

Beck, J. L. and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993-1002.

Berry, J. D. and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. Journal of Wildlife Management 49:237-240

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com/htools.

Beyer, A. C., M. A. Foster, and H. S. Denson. 2010. Upland game bird surveys, inventory and management: July 1, 2006–June 30, 2010. Montana Department of Fish, Wildlife & Parks Pittman-Robertson Report.

Bird, K. L., C. L. Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2012. The secret sex lives of sage-grouse: multiple paternity and intraspecific nest parasitism revealed through genetic analysis. Behavioral Ecology 24:29-38.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481-506.

Braun, C. E., T. E. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. Wildlife Society Bulletin 5:99-106.

Bureau of Land Management [BLM]. 2013. BLM Handbook, H-1624-1 – Planning for Fluid Mineral Resources, Rel/ 1-1749.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. Second edition. Springer-Verlag Inc., New York, USA.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388-394.

Centers for Disease Control (CDC). 2013. Statistics, surveillance, and control archive: West Nile virus. http://www.cdc.gov/ncidod/dvbid/westnile/surv&control_archive.htm.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of greater sage-grouse nests identified by video monitoring. Journal of Field Ornithology 79:421-428.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240-248.

Coggins, K. A. 1998. Relationship between habitat changes and productivity of sage grouse at Hart Mountain National Antelope Refuge, Oregon. Thesis, Oregon State University, Corvallis, USA.

Connelly, J. W., Jr. 1982. An ecological study of sage grouse in southeastern Idaho. Dissertation, Washington State University, Pullman, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000*a*. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52:116-122.

Connelly, J. W., M. L. Commons-Kemner, J. L. Beck, K. P. Reese, E. O. Garton, N. A. Burkepile, M. B. Lucia. 2006. Sage-grouse ecology. Idaho Department of Fish and Game, Boise, USA.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by sage grouse in southeastern Idaho. Condor 95:1041-1043.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011*a*. Characteristics and dynamics of greater sage-grouse populations. Pages 53-67 *in* S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Cooper Ornithological Society and University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, C. E. Braun, W. L. Baker, E. A. Beever, T. J. Christiansen, K. E. Doherty, E. O. Garton, C. A. Hagen, S. E. Hanser, D. H. Johnson, M. Leu, R. F. Miller, D. E. Naugle, S. J. Oyler-McCance, D. A. Pyke, K. P. Reese, M. A. Schroeder, S. J. Stiver, B. L. Walker, and M. J. Wisdom. 2011*b*. Conservation of greater sage-grouse: a synthesis of current trends and future management. Pages 549-563 *in* Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Cooper Ornithological Society and University of California Press, Berkeley, USA.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, M. A. Schroeder. 2003. Monitoring of Greater Sage-Grouse Habitats and Populations. Station Bulletin 80. College of Natural Resources Experiment Station Moscow, Idaho. S.D. Laursen director. University of Idaho, Moscow, USA.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011*c*. Characteristics of greater sage-grouse habitats: a landscape species at micro- and macroscales. Pages 69-83 *in S. T.* Knick, and J. W. Connelly, editors. Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Cooper Ornithological Society and University of California Press, Berkeley, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000*b*. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Cooch, E., and G. White. 2010. Known-fate models. Chapter 16 *in* Program MARK: a gentle introduction. 9th Edition. Cooch, E. and G. White, editors. Available from http://www.phidot.org/software/mark/docs/book/

Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395-405.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse habitat. Journal of Range Management 57:2-19.

Crunden, C. W. 1963. Age and sex of grouse from wings. Journal of Wildlife Management 27:846-849.

Dahlgren, D. K. 2009. Greater sage-grouse ecology, chick survival, and population dynamics, Parker Mountain, Utah. Dissertation, Utah State University, Logan, USA.

Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010*a*. Achieving better estimates of greater sage-grouse chick survival in Utah. Journal of Wildlife Management 74:1286-1294.

Dahlgren, D. K., T. A. Messmer, E. T. Thacker, and M. R. Guttery. 2010*b*. Evaluation of brood detection techniques: recommendations for estimating greater sage-grouse productivity. Western North American Naturalist 70:233-237.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage-grouse in Idaho. Journal of Wildlife Management 27:811-841.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science 33:43-64.

Delong, A. K., J. A. Crawford, and D. C. Delong, Jr. 1995. Relationships between vegetation structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59:88-92.

Doherty, K. E., D. E. Naugle, and J. S. Evans. 2010. A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. PLoS One 5:e10339.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994*a*. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54:170–176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994*b*. Diets and food selection of sage grouse chicks in Oregon. Journal of Range Management 47:90-93.

Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621–627.

Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile sage grouse. Journal of Wildlife Management 50:228–235.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Fedy, B. C., C. L. Aldridge, K. E. Doherty, M. O'Donnell, J. L. Beck, B. Bedrosian, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. McKee, C. Olson, C. C. Swanson, B. L. Walker. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management 76:1062-1071.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996. Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. Condor 98:868-872.

Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the Northern Great Basin. Journal of Wildlife Management 73:904-913.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. Delong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radio transmitters to estimate survival of Greater Sage-Grouse chicks. Journal of Wildlife Management 71:646-651.

Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and renesting by greater sage-grouse. Journal of Wildlife Management 70:472-478.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitat. Wildlife Biology 13:42-50.

Herman-Brunson, K. M. 2007. Nesting and brood-rearing success and habitat selection of greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. Thesis, South Dakota State University, Brookings, USA.

Herman-Brunson, K. M., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology 15:395-404.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Hornaday, W. T. 1916. Save the sage grouse from extinction, a demand from civilization to the western states. New York Zoological Park Bulletin 5:179-219.

Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. Thesis, Colorado State University, Fort Collins, USA.

Huwer, S. L., D. R. Anderson, T. E. Remington, and G. C. White. 2008. Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. Journal of Wildlife Management 72:1622-1627.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis, South Dakota State University, Brookings, USA.

Keppie, D. M. 1977. Inter-brood movements of juvenile spruce grouse. Wilson Bulletin 89:67-72.

Kirby, D. R., and K. L. Grosz. 1995. Cattle grazing and sharp-tailed grouse nesting success. Rangelands 17:124-126.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. The Condor 114:75-89.

Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649-662.

Knick, S. T., and J. W. Connelly. 2011. Greater sage-grouse and sagebrush: an introduction to the landscape. Pages 1-9 *in* Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Cooper Ornithological Society and University of California Press, Berkeley, USA.

Lacy, R. C., M. Borbat, and J. P. Pollak. 2003. VORTEX: A Stochastic Simulation of the Extinction Process. Version 9. Chicago Zoological Society, Brookfield, IL, USA.

Martin, N. S. 1970. Sagebrush control related to habitat and sage grouse occurrence. Journal of Wildlife Management 34:313-320.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McCarthy, J. J. 2003. Results from the use of a system of "rest rotational grazing" for livestock to improve wildlife habitat in Montana. Journal of Mountain Ecology 7:13-16.

Mezquida, E. T., S. J. Slater, and C. W. Benkman. 2006. Sage-grouse and indirect interactions: potential implications of coyote control on sage-grouse populations. The Condor 108:747-759.

Miller, P. S., and R. C. Lacy. 2005. VORTEX: a stochastic simulation of the extinction process. Version 9.50 user manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, Minnesota, USA.

Montana Sage Grouse Work Group. 2005. Management plan and conservation strategies for sage grouse in Montana – final. Rev 2-1-2005.

Montana's Greater Sage-grouse Habitat Conservation Advisory Council. 2013. Draft greater sage-grouse habitat conservation strategy. http://fwp.mt.gov/fishAndWildlife/management/sageGrouse/habitatConservation/.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north central Montana. Dissertation, University of Montana, Missoula, USA.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. Journal of Wildlife Management 71:1773-1783.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. Ecological Applications 16:1529-1538.

Natural Resources Conservation Service [NRCS]. 2010. Greater sage-grouse habitat conservation strategy: core area 13 map. http://www.mt.nrcs.usda.gov/technical/ecs/biology/sagegrouse/sagegrouse_strategy.html.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. T. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: a pending crisis for Greater Sage-Grouse. Ecology Letters 7:704-713.

Naugle, D. E. C. L. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: what more have we learned? Wildlife Society Bulletin 33:616-623.

Naugle, D. E., K. E. Doherty, B. L. Walker, H. E. Copeland, M. J. Holloran, and J. D. Tack. 2011. Sage-grouse and Cumulative Impacts of Energy Development. Pages 55-70 *in* Energy Development and Wildlife Conservation in Western North America. Island Press, Washington DC, USA.

National Oceanic and Atmospheric Administration [NOAA]. 2013. National Climactic Data Center climate data online search tool. http://www.ncdc.noaa.gov/cdo-web/search.

Neudecker, G. A., A. L. Duvall, and J. W. Stutzman. 2011. Community-based landscape conservation: a roadmap for the future. Pages 211-230 *in* Naugle, D.E. editor. Energy Development and Wildlife Conservation in Western North America. Island Press, Washington DC, USA.

North Dakota State Climate Office. 2011. North Dakota monthly climate summary, May 2011. http://www.ndsu.edu/ndsco/publication/ndsco/summary/2011/may.pdf.

Patterson, R. L. 1952. The sage-grouse in Wyoming. Sage Books, Inc., Denver, Colorado, USA.

Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147-155.

Rebholz, J. L. 2007. Influence of habitat characteristics on greater sage-grouse reproductive success in the Montana Mountains, Nevada. Thesis, Oregon State University, Corvallis, USA.

Rebholz, J. L., D. W. Robinson, and M. D. Pope. 2009. Nest site characteristics and factors affecting nest success of greater sage-grouse. The Open Ornithology Journal 2:1-6.

Remington, T. E., and C. E. Braun. 1985. Sage grouse food selection in winter, North Park, Colorado. Journal of Wildlife Management 49:1055-1061.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.

Robertson, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southern Idaho. Thesis, University of Idaho, Moscow, ID.

Rohlf, F. J., and R. R. Sokal. 1981. Statistical Tables. 2nd edition. W. H. Freeman and Company, New York, USA.

Rotella, J. 2010. Nest survival models. Ninth edition. Pages 17-1 to 17-20 *in* Cooch, E., and G. White, editors. Program MARK: a Gentle Introduction. http://www.phidot.org/software/mark/docs/book/.

Saether, B. E., and A. Bakke. 2000. Avian life-history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Samuel, M. D., and M. R. Fuller. 1996. Wildlife radiotelemetry. Fifth edition. Pages 370-418 *in* T. A. Bookhout, editor. Research and Management Techniques for Wildlife and Habitats. The Wildlife Society, Bethesda, Maryland, USA.

Schoenberg, T. J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Michell, E. V. Rickerson and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363-376.

Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24-32.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291-299.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The Birds of North America, Number 425. The Birds of North America, Philadelphia, Pennsylvania, USA.

Sika, J. L. 2006. Breeding ecology, survival rates and mortality causes of hunted and non-hunted greater sage-grouse in central Montana. Thesis, Montana State University, Bozeman, USA.

Smith, R. E. 2013. Conserving Montana's sagebrush highway: long distance migration in sage-grouse. Thesis, University of Montana, Missoula, USA.

Southwood, T. R. E., and D. J. Cross. 2002. Food requirements of grey partridge *Perdix perdix* chicks. Wildlife Biology 8:175-183.

Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58:344–351.

Swanson, C. C. 2009. Ecology of greater sage-grouse in the Dakotas. Dissertation, South Dakota State University, Brookings, USA.

Swanson, C. C., M. A. Rumble, T.W. Grovenburg, N. W. Kaczor, R. W. Klaver, K. M. Herman-Brunson, J. A. Jenks, and K. C. Jensens. 2013. Greater sage-grouse winter habitat use on the eastern edge of their range. Journal of Wildlife Management 77:486-494.

Tack, J. D., D. E. Naugle, J. C. Carlson, and P. J. Fargey. 2011. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: a biological basis for international prairie conservation. Oryx 46:64–68.

Taylor, R. L., D. E. Naugle, and L. S. Mills. 2010. Viability analyses for conservation of sage-grouse populations. Completion report to the Bureau of Land Management, Miles City, Montana, USA.

Taylor, R. L., B. L Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize Greater Sage-Grouse population growth. Journal of Wildlife Management 76:336-347.

United States Environmental Protection Agency [EPA]. 2004. Wetlands and West Nile virus. http://www.epa.gov/owow/wetlands/pdf/WestNile.pdf.

U. S. Fish and Wildlife Service. 2010. 12-month findings for petitions to list the Greater Sage-Grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Registry 75:13910-14014.

U.S. Fish and Wildlife Service. 2011. Greater sage-grouse: fact sheet. http://www.fws.gov/home/feature/2012/pdfs/GreaterSageGrouseFactSheet.pdf.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425-426.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming. Dissertation, University of Montana, Missoula, USA.

Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-142 *in* S. T. Knick, and J. W. Connelly, editors. Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its

Habitats. Cooper Ornithological Society and University of California Press, Berkeley, USA.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. From the Field: outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007. West Nile virus and greater sage-grouse: estimating infection rate in a wild bird population. Avian Diseases 51:691-696.

Wallestad, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129–136.

Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Department of Fish and Game, and U.S .Department of Interior Bureau of Land Management, Helena, Montana, USA.

Westerkov, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56-67.

Wik, P. A. 2002. Ecology of Greater sage-grouse in south-central Owyhee County, Idaho. M.S. Thesis, University of Idaho, Moscow, USA.

Wyoming Game and Fish Department [WGFD]. 2010. Sage-Grouse Core Management Areas: Version 3. Wyoming Game and Fish Department. http://wgfd.wyo.gov/web2011/wildlife-1000382.aspx.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144-154.

Zou, L., S. N. Miller, and E. T. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coalbed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

Zwickel, F. C. 1967. Early behavior in young blue grouse. Murrelet 48:2-7.

– Appendix A –
Weather Conditions

Sage-grouse in southeastern Montana were exposed to extreme weather conditions throughout the study. Precipitation during spring/summer 2010 was 53% above average, which caused localized spring flooding and extraordinary growth of vegetation (Table A.1, Fig. A.1). Precipitation levels during spring/summer 2011 were even higher, 67% above normal levels. Eight inches of precipitation were received during the month of May alone. This heavy precipitation combined with melting snow pack caused rivers to rise above the 100-year flood level and resulted in widespread flood events throughout the study area, eastern Montana, and the western Dakotas (North Dakota State Climate Office 2011; Table A.1, Fig. A.2). Conversely, above-average temperatures coupled with below-normal precipitation resulted in drought conditions during summer 2012 (Tables A.1 and A.2, Fig. A.3).

Table A.1. Spring/summer monthly precipitation totals, and normal (30-year average; 1983–2012) monthly precipitation from the Ridgeway, Montana weather station (station ID USC00247034, NOAA 2013).

	Monthly precipitation (inches)				
Month	2009	2010	2011	2012	Normal
March	1.8	1.0	0.8	0.1	0.6
April	1.3	2.4	2.6	1.7	1.4
May	1.3	3.7	8.0	1.6	2.3
June	3.0	5.3	3.4	1.6	2.4
July	2.6	2.7	1.1	3.0	1.6
August	1.7	0.9	2.8	0.9	1.3
September	0.6	1.8	0.2	0.2	1.2
October	1.5	0.3	1.0	1.1	1.0
Total	*13.8*	*18.2*	*19.9*	*10.3*	*11.9*



Figure A.1. Extraordinary precipitation during spring/summer 2010 and 2011 resulted in tremendous growth of vegetation during both years. Note the sage-grouse hen in the lower right corner of the photo.



Figure A.2. The Little Missouri River north of Albion, MT rose above 100-year flood levels during spring 2011.

Table A.2. Spring/summer monthly average temperatures, and normal (30-year average; 1983–2012) monthly temperatures from the Ridgeway, Montana weather station (station ID USC00247034, NOAA 2013).

	Temperature (°F)				
	2009	2010	2011	2012	Normal
March	28.0	34.5	28.6	47.1	32.9
April	39.0	45.7	43.0	48.2	43.8
May	53.8	50.9	50.0	54.1	53.6
June	59.4	62.6	62.1	69.1	63.1
July	68.0	68.9	73.9	77.0	71.2
August	65.5	69.3	70.3	69.3	69.5
September	63.9	57.7	59.5	60.1	58.7
October	37.9	50.5	49.1	42.6	45.0
Average	*51.9*	*55.0*	*54.6*	*58.4*	*54.7*



Figure A.3. Below-average precipitation and above-average temperatures resulted in drought conditions during summer 2012. Note that abundant residual cover was left over from wet conditions during spring/summer 2011.

Above-average snowfall and below-average temperatures occurred during winter 2009–10. The following winter, 2010–11, was among the most severe on record (30 year winter event; Tables A.3, A.4). Snowfall during winter 2010–11 was nearly 3 times normal levels (Table A.3). Snow completely covered shrubs and vegetation throughout much of the Core Area (Fig. 1.2), and in some places snow drifts were deep enough to bury fence lines (Fig. A. 4). In contrast, winter 2011–12 was among the mildest on record with low levels of snowfall, above-average temperatures, and completely open winter conditions (Tables A.3, A.4, Fig. A.5).

Table A.3. Total monthly snowfall, and normal (30-year average; 1983–2012) monthly snowfall from the Ridgeway, Montana weather station (station ID USC00247034, NOAA 2013).

	Snowfall (inches)				
	2009–10	2010–11	2011–12	2012–2013	Normal
November	2.0	19.1	4.0	2.0	6.4
December	16.0	6.9	6.0	12.0	6.8
January	9.0	21.0	8.0	9.0	7.0
February	9.0	22.0	5.0	1.0	5.9
Total	*36.0*	*69.0*	*23.0*	*24.0*	*26.2*

Table A.4. Winter monthly average temperature, and normal (30-year average; 1983–2012) monthly average temperatures from the Ridgeway, Montana weather station (station ID USC00247034, NOAA 2013).

	Temperature (°F)				
	2009–10	2010–11	2011–12	2012–2013	Normal
November	37.2	26.8	31.3	35.2	31.1
December	12.6	17.2	25.5	19.4	19.9
January	16.0	16.0	24.6	17.8	19.4
February	13.8	12.9	23.5	27.9	22.7
Average	*19.9*	*18.2*	*26.2*	*25.1*	*23.3*



Figure A.4. Snowfall during winter 2010–11 was nearly 3 times average, resulting in a vast snowscape and deep snow drifts throughout the Core Area.



Figure A.5. Above-average temperatures and below-average snowfall during winter 2011–12 resulted in mild, open conditions.

Grazing Capacity and Stocking Rate

DEE GALT, FRANCISCO MOLINAR, JOE NAVARRO, JAMUS JOSEPH, AND JERRY HOLECHEK

During the past 5 years grazing capacity surveys have been increasingly used in range management decisions on both public and private lands in the western United States. They are also becoming more used in developing countries such as South Africa, Australia, Brazil, and Mexico. Range professionals and ranchers are better recognizing that successful range management depends on stocking rangelands so adequate vegetation residues remain to protect rangeland health, maintain multiple values, and insure economic viability. Recently there has been growing support for changes in existing government programs as well as new programs that would encourage conservative grazing on both public and private rangelands. Sound stocking rate and grazing capacity procedures will be essential if these programs are to be successfully implemented.

Government subsidies for brush control and seeding on both public and private lands are now under intensive attack from environmental groups...

What is Grazing Capacity?

Generally, grazing capacity is considered to be the average number of animals that a particular range or ranch will sustain over time. It is based on stocking rate. Stocking rate is defined by the Society for Range Management as the amount of land allocated to each animal unit for the grazable period of the year. Determination of stocking rate and grazing capacity involve the same procedures, except that grazing capacity estimates require adjustment of forage production to the hypothetical average year. We define this hypothetical average year as the average forage production for the previous 10 year period. Ideally, at least 3 years of forage production data should be collected to establish grazing capacity. However, in reality this is often not possible due to management requirements for immediate information and/or funding limitations. Regression equations relating forage production to monthly and annual precipitation have been developed for specific range types. **We have found them to be reasonably reliable if no major aberrations occur in precipitation during the survey year. We do caution that grazing capacity is part myth and part reality: The average number of livestock a ranch has carried over the previous 5, 10, or 20 years may have little relevance to what it will support in any given year or group of years.**

Applications of Grazing Capacity

Under present policy, livestock grazing permits on federal lands in the USA are reviewed for renewal every 10 years. They also undergo review when the permit is transferred to another owner. The most basic decision on the new permit is the number of animal units that will be assigned to the allotment. This is the basis for value of the permit and grazing fees the rancher will pay. **The best approach to determining safe stocking rate on rangelands is knowing the numbers of animals actually grazing a ranch or allotment over a period of years together with utilization levels, range trend analyses, and precipitation records.** Incomplete and/or uncertain information on livestock numbers actually grazed, grazing use, and trend has created the demand for formal grazing capacity surveys to better establish the appropriate permit number. Increasingly, environmental groups are participating in the permit renewal process. They are prepared to challenge any decision not based on sound information and, in some cases, those that do have a sound basis. These forces have increased the need for formal grazing capacity determinations based on the best available science.

There is considerable turnover of both public and private land ranches in New Mexico and most other western states. Financial success in ranching depends on buying grazing capacity at or below fair market value and properly stocking the ranch after purchase. Ranch buyers are increasingly recognizing that realtor statements, ranch financial records, and public land grazing permits do not necessarily accurately reflect grazing capacity. Another problem is that location and extent of forage resources within ranches or allotments are often poorly identified and quantified. A good grazing capacity survey not only helps to establish ranch value, but it also provides valuable information on infrastructure (water, fence, roads, corrals); ecological condition of various pastures; land unsuited for grazing due to terrain, distance from water, and other constraints; past range use; range trend; noxious plant problems; and wildlife grazing use. Information on key forage species and key areas for monitoring precipitation, trend, grazing use, and forage production should be routinely provided in a grazing capacity survey. Generally, we believe once a grazing capacity survey is conducted, it should be updated every 10 years.

Grazing Capacity Procedures

Specific procedures for setting stocking rates and establishing grazing capacity are generally well developed. Issues such as key area selection, quantification of forage production, selection of harvest coefficients, corrections for slope and distance to water, and animal forage intake allowances are thoroughly discussed by these papers. However, we believe selection of the harvest coefficient and corrections for slope and distance from water merit further discussion.

Harvest Coefficient Selection

The harvest coefficient is the percentage of total forage produced that is assigned to grazing animals for consumption. Holechek (1988) bases harvest coefficient selection on various stocking rate studies from different range types. For most arid and semi-arid areas, a harvest coefficient of 35% would be selected while 50% would usually be used for annual grasslands and humid areas.

An alternative, more simple approach involves assigning 25% of the forage to livestock, 25% to wildlife and natural disappearance, and 50% for site protection. This procedure is obviously more restrictive.

We have had the opportunity to make detailed evaluations of actual forage use when the Holechek stocking procedure was applied on several New Mexico rangelands. Consistently, actual measured use has been 10–15% higher than the intended use. We attribute this to livestock trampling, wildlife consumption, and weathering. On Chihuahuan Desert rangelands, Paulsen and Ares recommended that stocking levels be set for 35% use of perennial grasses. However, they noted that the harvest coefficient must be set at 30% to obtain 35% use because of trampling, wildlife, and weathering losses. Past and recent research has confirmed this wisdom.

Over an 8 year period, pastures on the Chihuahuan Desert Rangeland Research Center in south-central New Mexico assigned a 30% harvest coefficient, carried nearly as many cattle as those assigned a 40% harvest coefficient. This was because conservatively stocked pastures produced more forage in drought years and required less destocking. There has also been a substantial improvement in ecological range condition and forage production on the conservatively stocked pastures over time. Cattle productivity was substantially higher in the conservatively stocked pastures.

We increasingly hold the opinion that a 25% harvest coefficient is a sound idea for most western rangelands. After careful analysis of their own and existing research, Johnston et al. recommended a 25% harvest coefficient for Australian rangelands. It allows both forage species and livestock to maximize their productivity, allows for error in forage production estimates, greatly reduces problems from buying and selling livestock, reduces the risk of financial ruin during drought years, and promotes multiple use values.

In the Chihuahuan Desert of New Mexico, the rancher who routinely stocks at capacity based on a 25% harvest coefficient will need to liquidate or dry lot feed about one half their herd in 2 years out of 10 (Table 1). In contrast, the rancher using a 35% harvest coefficient will need to completely destock in 2 years out of 10 and partially destock in another 1–2 years. We acknowledge that ranchers in the more humid Great Plains rangelands may do better with a 35% than 25% harvest coefficient because of less annual variation in forage production.

The authors research and experience across a variety of landscapes, ranches, and countries shows a 25% harvest coefficient is the surest way to avoid chronic forage deficits and land degradation. Any financial advantages of higher harvest coefficients become doubtful in arid and semi-arid areas if a 10 year or more time horizon is used.

The real problem is that few ranchers have the skills or time/labor resources to annually quantify forage production. Unless this is done, use of higher harvest coefficients than 25% invariably leads to land degradation and severe financial losses when drought occurs because of rancher reluctance to destock. These losses can quickly eliminate any accumulated benefits of more efficient forage use. Unused forage in wet years provides a reserve of forage for drought and increases plant vigor and soil water infiltration. Rather than a waste, we see it as an investment in the future. New Mexico research shows conservative stocked rangelands produced nearly 50% more forage than moderate stocked rangelands in drought years. Studies from other range types validate these findings. Early studies showed unused residue can increase forage production by 50% or more compared to areas where it is removed by grazing.

Table 1. Ten year variation in forage production on moderately grazed New Mexico Chihuahuan Desert and Colorado mid-grass prairie rangelands.

	Chihuahuan Desert New Mexico[1]			Mid-Grass Prairie Colorado[2]	
Year	Annual precipitation	Forage production	Year	Annual precipitation	Forage production
	(inches)	(lbs/acre)		(inches)	(lbs/acre)
1989	7.6	189	1957	13.2	1141
1990	10.7	270	1958	17.3	1489
1991	15.1	488	1959	13.5	1095
1992	15.4	750	1960	12.5	1140
1993	9.9	203	1961	17.9	1508
1994	7.0	6	1962	16.4	1314
1995	6.7	59	1963	18.7	1327
1996	7.9	145	1967	9.9	1179
1997	11.6	284	1965	19.4	1197
1998	8.2	173	1966	13.8	1267
Average	10.0	257		15.3	1266
Standard deviation	3.0	207		2.9	137
Coefficient variation	30.2	81		18.9	11

[1]Source: Holechek et al. 1999
[2]Source: Sims et al. 1976

Some of the most successful ranchers we have encountered have their operations in the Chihuahuan Desert of northern Mexico. Although we found none of them ever took any classes in grazing management, this family has well over 100 years of ranching experience. They are firm believers in light to conservative use of their forage and well distributed watering points. This allows them to maintain their herds with little destocking in the worst of drought years. They shuffle their cattle around to where forage growth is best by manipulating access to water resources. We were amazed at how good their rangeland and cattle looked in the dry years of the mid 1990's (Figure 1).

Heitschmidt and Walker suggested that plant species composition does not impact society's acceptance of a given grazing practice nearly as much as amount of standing biomass, ground cover, number of fecal patties, and so on. They believed grazing technology in the 21st century will depend heavily on managing residue levels to insure a variety of multiple use values. We believe the 25% harvest coefficient accomplishes this goal quite well.

Slope Adjustments

Although the need to adjust grazing capacity for distance from water and slope has long been recognized, Holechek (1988) provides the first formal procedures for these adjust-

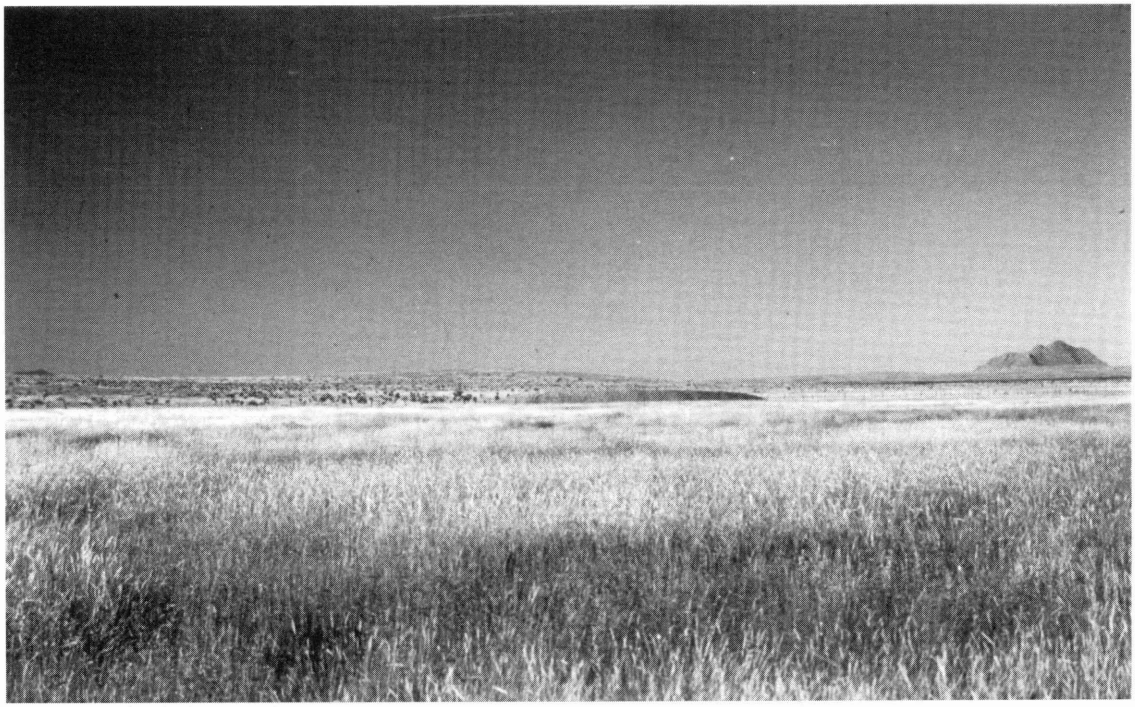


Fig. 1. ***This Chihuahuan Desert ranch in northern Mexico has a long history of light to conservative stocking. Vegetation is in near climax and the ranch owners have had to do little destocking in dry years. Primary forage grasses in picture are black grama and tobosa.***

ments we have found in the literature. His reductions are well supported by previous and present research. Most recently, the United States Department of Agriculture—Natural Resources Conservation Service has adopted Holechek's guidelines. His guidelines involve no reduction for 0–10% slopes, 30% reduction for 11–30% slopes, 60% reduction for 31–60% slopes, and 100% reduction for slopes over 60%. In our grazing capacity surveys in New Mexico we have found Holechek's guidelines to work quite well when actual use was checked against intended use. However, we do believe ranchers who obtain more uniform use of rugged terrain than would be expected should be given some flexibility on slope reductions if they document pasture use patterns.

Educational Benefits

In our opinion, one of the greatest benefits of a grazing capacity survey is that it creates an opportunity to educate ranchers on range management. During their participation in designing and implementing the survey, most new and many experienced ranchers greatly improve their capability to make sound stocking rate decisions.

From this point, the next steps are establishing a program for rangeland monitoring and a plan to deal with drought. Utilization levels can be practically monitored by the rancher. Through use of the key sites that are representative of the pasture and 0.75 to 1.00 mile from water, qualitative grazing intensity assessments can be made. Percent use of forage can be determined by general appearance of the range at the end of the grazing period. Intensity can also be substantiated by stubble height measurements of key forage species and weight estimates of forage residues remaining on the land. Rain gauges distributed over the pasture can be helpful in assessing forage production and managing drought situations. A sound monitoring program provides many benefits to livestock producers over the long term. It is our experience when ranchers fully consider the problems associated with liquidating and reacquiring livestock during and after drought, their attitudes on stocking rate and grazing capacity change. They better accept the realities of arid land ranching and are more prone to select "safe" or conservative stocking rates.

Political Backdrop

It is our observation that the whole focus of range management on public and private lands from the 1950's through the 1980's has centered around keeping stocking rates as high as possible through ranch capitalization (water development, fence, brush control, seeding), often subsidized by the federal government. By the 1990's many ranchers were fully capitalized with water and fence.

Government subsidies for brush control and seeding on both public and private lands are now under intensive attack from environmental groups and are being questioned by members of the range management and ranching communities. Increased enforcement of the Endangered Species Act and the National Environmental Policy Act have made application of various range improvements on public lands more difficult. During the past 20 years brush encroachment has severely reduced forage production on many western rangelands where pinyon-juniper, sagebrush, and other shrubs had been controlled in the 1950's, 1960's, and 1970's (Figure 2).

During the early 1980's the Savory Grazing Method provid-

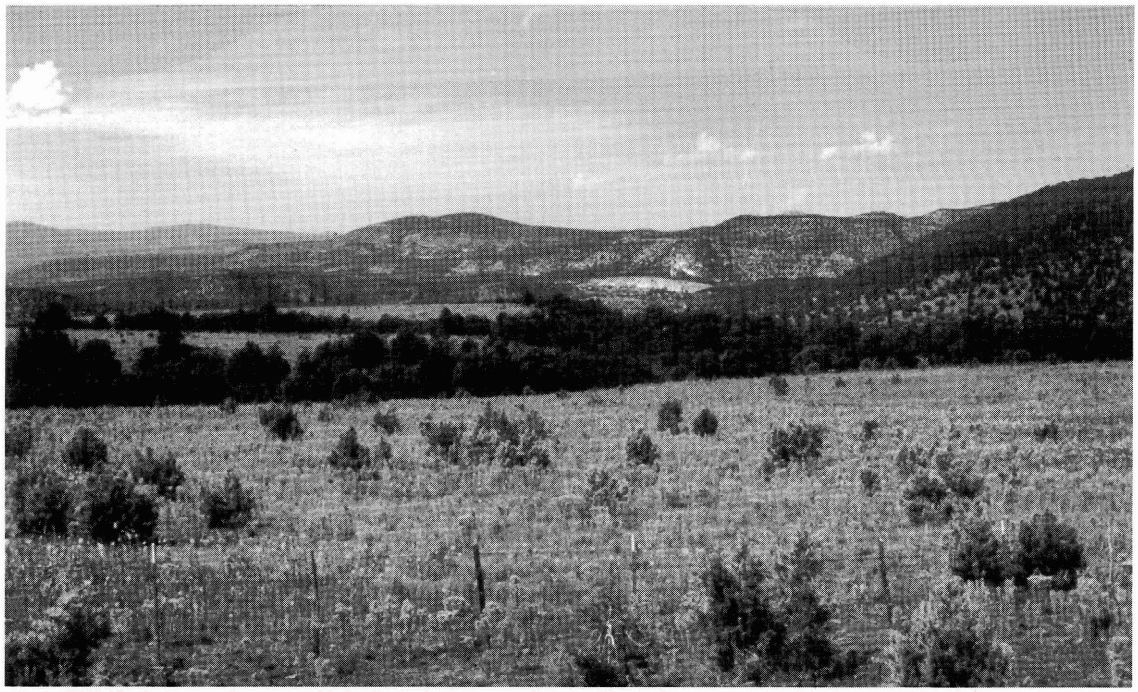


Fig. 2. ***Encroachment of pinyon-juniper into grasslands is reducing grazing capacity on many New Mexico rangelands. Tree control has become more difficult due to government regulations, reductions in subsidies, and higher costs for improvement. This has necessitated better balancing of animal numbers to existing forage supplies.***

ed hope that ranchers could increase their grazing capacity and stocking rates concurrently without use of brush control or seeding. Research has shown that it may not have any stocking rate or forage production advantages over other grazing systems that have been developed (Holechek et al. 1999).

Recently, more environmental leaders, range professionals, and ranchers have advocated conservative stocking as a win-win approach to concurrently increasing grazing capacity and multiple use values. Research showing that conservative stocking can be an effective, low cost way to increase grazing capacity is hardly new. Early studies convincingly showed its biological and financial benefits. The problem has long been that the idea of stocking reductions as a means to increased grazing capacity, has never played well with the ranching community. This is particularly true with large public land ranchers whose net worth and security of grazing privileges are closely associated with livestock numbers specified on their grazing permit. Various reforms have been proposed to remedy this problem, but so far none have been put into legislation.

In spite of resistance from some ranchers and range professionals, balancing animal numbers with existing forage supplies rather than expanding forage supplies through range improvements was increasingly used on public rangelands in New Mexico in the 1990's. Low cattle prices, rising ranching costs, and reductions in range improvement cost sharing subsidies have caused many private land ranchers to consider and apply this same approach. Hence, the new emphasis on establishing grazing capacity and using it as a basis for range management decisions as we move into the 21st century.

Analysis and Implications

We believe that in the 21st century, various range management decisions on public and private rangelands will depend heavily on grazing capacity surveys. Over the past 10 years several similar scientifically based procedures for determining stocking rates and grazing capacity have been developed. They are becoming somewhat standardized on animal intake rates, forage production determination, key area selection, and adjustments for slope and distance from water. Many range professionals now advocate a 25% harvest coefficient when grazing capacity and stocking rates are assigned. We believe this idea has considerable merit for arid and semi-arid areas from vegetation, livestock production, and multiple use standpoints.

Grazing capacity surveys provide a basis for ranch value, annual adjustments in stocking rates, grazing fees on public lands, and may soon be used in administration of subsidies that promote conservative stocking. They can also play an important role in allocation of forage to livestock and wildlife. While a sound grazing capacity survey can help establish the number of livestock a ranch will support through time, it must always be recognized that grazing capacity may have little relevance to livestock numbers sustainable in a given year or group of years. Although a good grazing capacity survey can be helpful in many range management decisions, it should not become a replacement for information on range trend, grazing use, and range condition.

References and Other Reading

Anderson, C. 1994. Overgrazing destroys income-producing rangeland. Texas Section, Society for Range Management, Grass Roots p. 7.

Beutner, E. L. and D. Anderson. 1943. The effect of surface mulches on water conservation and forage production in some semi-desert grassland soils. J. Amer. Soc. Agron. 33:393–400.

Heitschmidt, R. K. and J. W. Walker. 1996. Grazing management: Technology for sustaining rangeland ecosystems. Austr. Rangel. J. 18:194–215.

Holechek, J. L. 1988. An approach for setting the stocking rate. Rangelands 10:10–14.

Holechek, J. L. and D. Galt. 2000. Grazing intensity guidelines. Rangelands 21:(3)11–14.

Holechek, J. L. and K. Hess. 1994. Free market policy for public land grazing. Rangelands 16:63–67.

Holechek, J. L. and K. Hess, Jr. 1996. Market forces would benefit rangelands. Forum for Appl. Res. and Public Policy 2:5–15.

Holechek, J. L., M. Thomas, F. Molinar, and D. Galt. 1999. Stocking desert rangelands: What we've learned. Rangelands 21(6):8–12.

Holechek, J. L., H. Gomes, F. Molinar, D. Galt, and R. Valdez. 2000. Short-duration grazing: The facts in 2000. Rangelands 21(5):18–22.

Hutchings, S. S. and G. Stewart. 1953. Increasing forage yields and sheep production on intermountain winter ranges. U.S. Dep. Agric. Circ. 925.

Johnson, W. M. 1953. Effect of grazing intensity upon vegetation and cattle gains on ponderosa pine-bunchgrass ranges of the front range of Colorado. U.S. Dep. Agric. Circ. 929.

Johnston, P. W., G. M. McKean, and K. S. Daily. 1996. Objective 'safe' grazing capacities for southwest Queensland Australia. Aust. Rangel. J. 18:244–258.

Klipple, G. E. and R. E. Bement. 1961. Light grazing - Is it economically feasible as a range improvement practice? J. Range Manage. 14:57–62.

Klipple, G. E. and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on shortgrass ranges of the central Great Plains. U. S. Dept. Agr. Tech. Bull. 1216.

Lacey, J., E. Williams, J. Rolleri, and M. Marlow. 1994. A guide for planning, analyzing, and balancing forage supplies with livestock demand. Montana State Univ. Ext. Publ. EB-101.

Launchbaugh, J. L. 1957. The effect of stocking rate on cattle gains and on native shortgrass vegetation in west central Kansas. Kansas Agr. Exp. Sta. Bull. 394.

Martin, S. C. 1975. Stocking strategies and net cattle sales on semi-desert range. U.S. Dept. Agr. For. Serv. Res. Pap. RM-146.

Natural Resources Conservation Service. 1997. Range and Pasture Handbook. United States Dept. of Agr., Washington, DC.

Paulsen, H. A. and F. N. Ares. 1962. Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the southwest. U. S. Dept. Agr. Tech. Bull. 1270.

Schwan, H. E., J. Hodges, and C. N. Weaver. 1949. Influence of grazing and mulch on forage growth. J. Range Manage. 2:142–148.

Thurow, T. L. and C. Taylor, Jr. 1999. Viewpoint; The role of drought in range management. J. Range Manage. 52:413–419.

Troxel, T. R. and L. D. White. 1989. Balancing forage demand with forage supply. Texas A&M Univ. Ext. Serv. Publ. B-1606.

Valentine, K. A. 1970. Influence of grazing intensity on improvement of deteriorated black grama range. N. Mex. Agric. Exp. Stn. Bull. 553.

Ward, N. 1998. Sustainable ranching: A rancher's perspective. Rangelands 20(3):33–37.

Ward, N. 1999. Ranchers need support for sustainable ranching: What government can do: A rancher's perspective. Rangelands 21(3):13–17.

White, L. D. and A. McGinty. 1997. Stocking rate decisions. Texas A&M Univ. Agr. Ext. Serv. Publ. 13-5036.

Winder, J. A., C. C. Bailey, M. Thomas, and J. L. Holechek. 2000. Breed and stocking rate effects on Chihuahuan Desert cattle production. J. Range Manage. 53:32–38.

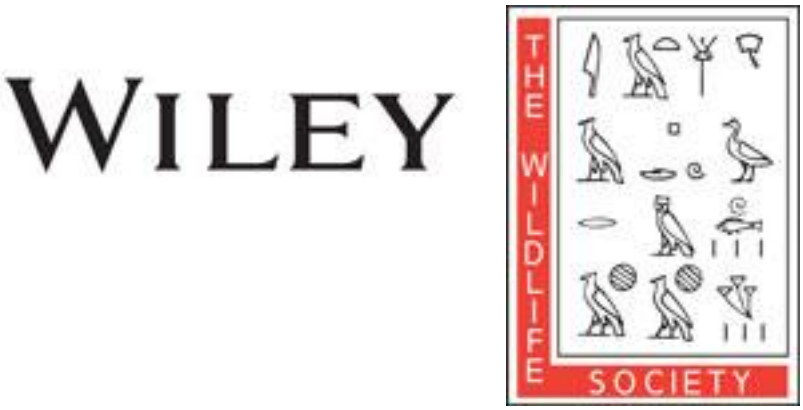
Authors are private range consultant, Las Cruces, New Mexico, 88005; assistant professor of range science, University of Juarez, Juarez, Mexico; and graduate research assistants and professor, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, New Mexico 88003. This paper was supported by the New Mexico Agricultural Experiment Station and was part of project 1-5-27417.

Statement of Ownership, Management, and Circulation
(Act. of August 12, 1970, Sec. 3685, Title 39, United States Code)

1. *Title of Publication*: Rangelands
2. *Date of Filing:* September 22, 2000
3. *Frequency of Issue*: Bimonthly
4. *Location of Office of Publication:* 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
5. *Location of General Business Office:* Same
6. *Name and Address of:*
   Publisher: Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
   Editor: Gary Frasier, 7820 Stag Hollow Road, Loveland, Colo. 80538
   Managing Editor: J. Craig Whitekiend, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
7. *Owner:* Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
8. *Known Bondholders, Mortgages, etc.:* Membership
9. *For Completion by Nonprofit Organizations Authorized to Mail at Special Rates:* The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes have not changed during preceding 12 months.
10. *Extent and Nature of Circulation*

	Avg. for 12 months	Actual for issue nearest filing date
A. *Total copies printed*	3,804	3,888
B. *Paid Circulation*		
1. *Dealers, counter sales*	0	0
2. *Mail subscriptions*	3,588	3,668
C. *Total paid circulation*	3,555	3.635
D. *Free distribution*	33	33
E. *Total distribution*	3,588	3,668
F. *Copies not distributed*	216	220
G. *Total*	3,804	3,888

I certify that the statements made by me above are correct and complete –*J. Craig Whittekiend,* Managing Editor.



Vegetational Cover and Predation of Sage Grouse Nests in Oregon
Author(s): Michael A. Gregg, John A. Crawford, Martin S. Drut and Anita K. DeLong
Source: *The Journal of Wildlife Management*, Vol. 58, No. 1 (Jan., 1994), pp. 162-166
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3809563
Accessed: 03-06-2016 14:27 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://about.jstor.org/terms

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Wiley, Wildlife Society are collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

M. Scott, eds. Estimating numbers of terrestrial birds. Cooper Ornithol. Soc., Stud. Avian Biol. 6.
U.S. FISH AND WILDLIFE SERVICE. 1988. Nongame bird strategies. Off. Migr. Bird Manage., Washington, D.C. 23pp.
WILEY, J. W. 1979. The white-crowned pigeon in Puerto Rico: status, distribution and movements. J. Wildl. Manage. 43:402–413.
———, AND B. N. WILEY. 1979. The biology of the white-crowned pigeon. Wildl. Monogr. 64. 54pp.
WOOD, D. A. 1992. Official lists of endangered and potentially endangered fauna and flora in Florida. Florida Game and Freshwater Fish Comm., Tallahassee. 25pp.

Received 5 October 1992.
Accepted 18 June 1993.
Associate Editor: Sauer.

VEGETATIONAL COVER AND PREDATION OF SAGE GROUSE NESTS IN OREGON

MICHAEL A. GREGG, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
JOHN A. CRAWFORD, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
MARTIN S. DRUT, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803
ANITA K. DELONG, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803

Abstract: Because of long-term declines in sage grouse (*Centrocercus urophasianus*) abundance and productivity in Oregon, we investigated the relationship between vegetational cover and nesting by sage grouse in 2 study areas. Medium height (40–80 cm) shrub cover was greater ($P < 0.001$) at nonpredated ($\bar{x} = 41\%$, $n = 18$) and predated ($\bar{x} = 29\%$, $n = 106$) nests than in areas immediately surrounding nests ($\bar{x} = 15$ and 10%, $n = 18$ and 106, nonpredated and predated, respectively) or random locations ($\bar{x} = 8\%$, $n = 499$). Tall (>18 cm), residual grass cover was greater ($P < 0.001$) at nonpredated nests ($\bar{x} = 18\%$) than in areas surrounding nonpredated nests ($\bar{x} = 6\%$) or random locations ($\bar{x} = 3\%$). There was no difference ($P > 0.05$) in grass cover among predated nests, nest areas, and random sites. However, nonpredated nests had greater ($P < 0.001$) cover of tall, residual grasses ($\bar{x} = 18\%$) and medium height shrubs ($\bar{x} = 41\%$) than predated nests ($\bar{x} = 5$ and 29% for grasses and shrubs, respectively). Removal of tall grass cover and medium height shrub cover may negatively influence sage grouse productivity.

J. WILDL. MANAGE. 58(1):162–166

Key words: *Centrocercus urophasianus*, habitat, nesting, Oregon, predation, reproduction, sage grouse, selection.

Sage grouse populations declined in several western states from the 1950s through the 1980s (Crawford and Lutz 1985, Klebenow 1985). In Oregon, the decrease in abundance of sage grouse was attributed to impaired productivity (Crawford and Lutz 1985). Reduced productivity may result from several factors, including excessive nest predation (Autenrieth 1981:39). Batterson and Morse (1948) and Nelson (1955) identified predation as the primary factor directly influencing sage grouse nesting success in Oregon. Although predators may be the immediate cause of nest loss, the amount and composition of vegetational cover at nests may influence predation (Bowman and Harris 1980, Redmond et al. 1982). We hypothesized that predation of sage grouse nests in Oregon was related to amount and composition of vegetational structural components surrounding nests. Our objective was to identify vegetational characteristics at nonpredated and predated sage grouse nest sites in comparison with randomly selected locations in 2 areas of southeastern Oregon.

Funds were provided by the Bureau of Land Management through a research contract administered by the Oregon Department of Fish and Wildlife. Logistical support was supplied by the U.S. Fish and Wildlife Service. We acknowledge J. K. Barnett and W. H. Pyle for assistance in data collection. We thank C. E. Braun, J. W. Connelly, R. L. Eng, D. A. Klebenow, K. P. Reese, and T. Rich for reviewing early drafts of this manuscript. This is Technical Paper 9839 of the Oregon Agricultural Experiment Station. Publication of this paper was sup-

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

ported, in part, by the Thomas G. Scott Achievement Fund.

STUDY AREAS

We conducted the study in 2 areas of southeastern Oregon: Hart Mountain National Antelope Refuge (Lake County) and Jackass Creek (Harney County). Topography of both areas consisted of flat sagebrush plains interrupted by rolling hills, ridges, and draws. Elevations ranged from 1,500 to 2,450 m at Hart Mountain and from 1,200 to 1,700 m at Jackass Creek. Mean maximum temperature (Mar–Aug) was 21 C at Hart Mountain and 24 C at Jackass Creek. Annual precipitation averaged 29 cm in both areas.

Vegetation at Hart Mountain and Jackass Creek consisted of low sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and western juniper (*Juniperus occidentalis*). Stands of aspen (*Populus tremuloides*), curl-leaf mountain-mahogany (*Cercocarpus ledifolius*), and bitter-brush (*Purshia tridentata*) occurred only at Hart Mountain. Common annual and perennial forbs included mountain-dandelion (*Agoseris* spp.), hawksbeard (*Crepis* spp.), milk-vetch (*Astragalus* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Grasses consisted mainly of bluegrass (*Poa* spp.), bluebunch wheatgrass (*Agropyron spicatum*), needlegrass (*Stipa* spp.), fescue (*Festuca* spp.), giant wildrye (*Elymus cinereus*), and bottlebrush squirreltail (*Sitanion hystrix*) (plant nomenclature from Hitchcock and Cronquist [1987]).

METHODS

From summer 1988 through spring 1991, we captured (Giesen et al. 1982) female sage grouse during July–August near watering areas and during March–April on and near leks. We fitted each hen with an aluminum leg band and a poncho-mounted, solar-powered radio transmitter with a nickel-cadmium battery (Amstrup 1980). The radio package (radio and poncho) weighed approximately 25 g. Juvenile females captured during summer were not marked with radios. We monitored radio-marked hens 3 times weekly throughout the nesting season with a hand-held antenna and portable receiver. When monitoring indicated a hen initiated a nest, visual confirmation was made without intentionally flushing the hen. Subsequently, we monitored hens remotely to avoid disturbance. When monitoring indicated a hen had ceased nesting efforts, we determined nest fate. We classified nests as nonpredated if ≥ 1 egg hatched or if incubation exceeded 30 days. Predated nests were identified by the presence of firmly attached shell membranes in broken eggs or by missing eggs.

We measured vegetation in a 78-m^2 area (circular area with a radius of 5 m) at nonpredated nest sites after completion of incubation and at predated nest sites on predicted hatch dates. We measured vegetation at randomly selected locations during early May. We located random sites with a random numbers table, which was used to determine starting points, compass bearing, and distance traveled. The number of random locations sampled in each study area was determined by canopy cover of sagebrush and sample size requirements (Snedecor and Cochran 1967:516). We measured canopy cover (%) of shrubs by line-intercept (Canfield 1941) along 2 10-m perpendicular transects intersecting at the nest or random location. The position of the first transect was determined from a randomly selected compass bearing. We placed each intercepted shrub into 1 of 3 height classes: short (<40 cm), medium (40–80 cm), or tall (>80 cm). We based height classes on results of previous studies (Nelson 1955, Wallestad and Pyrah 1974, Autenrieth 1981:17, Wakkinen 1990). Canopy cover of shrubs was recorded separately for each height class. We estimated cover (%) of forbs and grasses in 5 20- × 50-cm plots spaced equidistantly along each transect (Daubenmire 1959). We measured maximum droop height (excluding flowering stalks) of grasses at the nest bush and at random locations throughout each study area and classified grass genera as short (<18 cm) or tall (>18 cm), following results of Wakkinen (1990). We identified shrubs to species and forbs and grasses to genus.

To determine the relationship between vegetational features and predation of sage grouse nests, we apportioned the 78-m^2 area in which vegetational measurements were taken at each nest into 2 components: a 3-m^2 area at the nest and a 75-m^2 area immediately surrounding the nest. We used a factorial analysis of variance (ANOVA) and Student-Newman-Keuls multiple range tests adjusted for unequal sample sizes (Zar 1974:154) to compare vegetational characteristics among plot types (nonpredated nest and nest area, predated nest and nest area, and random location). Study area and year were additional factors in the ANOVA model to account for variation associated with spatial and tem-

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

poral differences. The only interactions were those for plot type by study area for forb ($P = 0.009$) and tall grass ($P < 0.001$) cover. However, individual ANOVAs coupled with Student-Newman-Keuls multiple range tests for these 2 variables by study area revealed identical patterns of mean separation, which indicated that these vegetational characteristics were not confounded by study area. Consequently, we assumed plot type was independent of study area. We detected no other interactions for any vegetational characteristic. Pearson correlation coefficients were used to test for intercorrelation among variables. All data were normally distributed, and we considered results significant if $P \leq 0.05$.

RESULTS

During 3 years, we located 124 sage grouse nests (57 at Hart Mountain and 67 at Jackass Creek); 18 of these were nonpredated (11 and 7 at Hart Mountain and Jackass Creek, respectively). Sage grouse nested in big sagebrush, low sagebrush, and mixed sagebrush (mosaic of big and low sagebrush) stands. Of 18 nonpredated nests, 13 were in big sagebrush stands, whereas only 3 and 2 nonpredated nests were in low and mixed sagebrush stands, respectively. Ninety-four percent of all nests from radio-marked hens were under sagebrush. Other vegetation used for nesting included rabbitbrush ($n = 5$), bitterbrush ($n = 1$), and giant wildrye ($n = 1$). Sagebrush collectively represented 87% of the shrub component in both study areas. Other shrubs included bitter-brush (6%), rabbitbrush (4%), horsebrush (*Tetradymia* spp.) (1%), and mountain snowberry (*Symphoricarpos oreophilus*) (1%). Tall grass genera included giant wildrye, wheatgrass, fescue, and needlegrass. Short grass genera consisted of bottlebrush squirreltail, junegrass (*Koleria cristata*), brome (*Bromus* spp.), and bluegrass.

Cover of tall grasses was greater ($P < 0.001$) at nonpredated nests than at predated nests or random locations (Table 1). No differences in grass cover were detected between predated nests and random sites. Except for one case, tall grasses at nonpredated nests were composed of residual cover.

For all nests, shrub cover of medium height was greater ($P < 0.001$) at nests than in the immediate area surrounding nests or random locations (Table 1). However, cover of medium height shrubs was greater ($P < 0.001$) at nonpredated nests than at predated nests. Furthermore, the immediate area surrounding nonpredated nest sites had greater ($P < 0.001$) cover of medium height shrubs than random locations. Shrub cover of short height was greater ($P = 0.02$) at predated nests than at random locations. Amount of tall grass was not correlated with short ($r = -0.06$) or medium ($r = 0.12$) shrub cover.

DISCUSSION

We found a relationship between vegetational cover and predation of sage grouse nests. Nonpredated nests had greater cover of tall, residual grasses and medium height shrubs than predated nests. No previous research demonstrated the value of residual grass cover at sage grouse nests, although its importance was suggested by Pyrah (1971) and Wakkinen (1990). Wakkinen (1990) reported data about grass height and nest fate but found no relationships. Our data, however, indicated that tall, residual grass cover may enhance sage grouse nest success. Grass cover was identified as an important nesting habitat component for other galliformes, including California quail (*Callipepla californica*) (Leopold 1977: 168), Attwater prairie-chickens (*Tympanuchus cupido attwateri*) (Lehman 1941:14), and plains sharp-tailed grouse (*T. phasianellus jamesi*) (Hillman and Jackson 1973:24). Lehman (1941: 14) noted that all prairie-chicken nests he located were in residual grass cover. The presence of tall, residual grass cover influenced nest site selection and nest predation rates of gray partridge (*Perdix perdix*) in Great Britain (Rands 1982).

We also demonstrated the importance of medium height shrub cover to successful nesting sage grouse. Wallestad and Pyrah (1974) found that successful nests had greater sagebrush cover than unsuccessful nests. Contrastingly, Autenrieth (1981:20) and Wakkinen (1990) found no relationship between canopy cover of sagebrush and nest fate. Hulet et al. (1986) reported that successful nests were located in areas of less shrub cover and shorter height sagebrush than nests that were predated.

Tall, dense, vegetational cover may provide scent, visual, and physical barriers between predators and nests of ground-nesting birds (Bowman and Harris 1980, Redmond et al. 1982, Sugden and Beyersergen 1987, Crabtree et al. 1989). Greater amounts of tall grasses and medium height shrubs at successful sage grouse

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

Table 1. Vegetational characteristics (% cover) at nonpredated and predated nests and areas immediately surrounding nests of radio-marked sage grouse, and random locations in southeastern Oregon, 1989–91.

	Nonpredated (n = 18)				Predated (n = 106)				Random (n = 499)	
	Nest[a]		Nest area[b]		Nest		Nest area			
Characteristic	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Grass cover										
Short, <18 cm	6A[c]	1.1	7A	1.2	6A	0.7	8A	0.5	8A	0.3
Tall, >18 cm	18A	5.5	6B	2.0	5B	1.2	3B	0.6	3B	0.2
Forb cover	8A	1.2	10A	1.4	9A	0.9	9A	0.5	9A	0.3
Shrub cover										
Short, <40 cm	14AB	3.9	15AB	2.7	19B	1.9	17AB	1.0	14A	0.4
Medium, 40–80 cm	41A	5.2	15B	3.3	29C	2.1	10BD	1.0	8D	0.4
Tall, >80 cm	1A	0.7	1A	0.7	4A	1.2	1A	0.3	3A	0.3

[a] 3-m^2 area at nest.
[b] 75-m^2 area immediately surrounding nest.
[c] Means with same letter within rows were not different $P \geq 0.05$.

nests likely provided the lateral and overhead concealment needed for security from predators. Nests lacking adequate cover were more likely to be predated. Our results confirmed the hypothesis of a relationship between vegetational cover and predation, but further investigation, in the form of controlled experimental tests, is needed to elucidate this principle.

MANAGEMENT IMPLICATIONS

Land management practices that decrease tall grass and medium height shrub cover at potential nest sites may be detrimental to sage grouse populations because of increased nest predation. Livestock grazing remains the most common and widespread use of rangelands in Oregon and is the principal land management practice and proximate factor that affects grass cover and height (Rickard et al. 1975). Grazing of tall grasses to <18 cm would decrease their value for nest concealment. Land management practices that affect medium height shrub cover include eradication of sagebrush for agricultural production, increased livestock forage, urban development, and mining activities (Klebenow 1972, 1985; Braun et al. 1977). Habitats that support the amount and type of grass cover needed for successful sage grouse nesting typically contain 8–12% shrub cover in Wyoming big sagebrush (*A. t. wyomingensis*) stands and 15–20% shrub cover in mountain (*A. t. vaseyana*) or basin (*A. t. tridentata*) big sagebrush stands (Winward 1991). Management activities should allow for maintenance of tall, residual grasses or, where necessary, restoration of grass cover within these stands.

LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. J. Wildl. Manage. 44:214–217.

AUTENRIETH, R. E. 1981. Sage grouse management in Idaho. Idaho Dep. Fish and Game, Boise. Wildl. Bull. 9. 238pp.

BATTERSON, W. M., AND W. B. MORSE. 1948. Oregon sage grouse. Oregon State Game Comm., Portland. Fauna Ser. 1. 29pp.

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest depredation. Ecol. Monogr. 38:269–308.

BRAUN, C. E., T. BRITT, AND R. O. WALLESTAD. 1977. Guidelines for maintenance of sage grouse habitats. Wildl. Soc. Bull. 5:99–106.

CANFIELD, R. H. 1941. Application of the line interception method in sampling of range vegetation. J. For. 39:386–394.

CRABTREE, R. L., L. S. BROOME, AND M. L. WOLFE. 1989. Effects of habitat characteristics on gadwall nest predators and nest-site selection. J. Wildl. Manage. 53:129–137.

CRAWFORD, J. A., AND R. S. LUTZ. 1985. Sage grouse population trends in Oregon, 1941–1983. Murrelet 66:69–74.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci. 33: 224–227.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildl. Soc. Bull. 10:224–231.

HILLMAN, C. N., AND W. W. JACKSON. 1973. The sharp-tailed grouse in South Dakota. South Dakota Dep. Game, Fish, and Parks, Pierre. Tech. Bull. 3. 64pp.

HITCHCOCK, C. L., AND A. CRONQUIST. 1987. Flora of the Pacific Northwest. Sixth ed. Univ. Washington Press, Seattle. 730pp.

HULET, B. V., J. T. FLINDERS, J. S. GREEN, AND R. B. MURRAY. 1986. Seasonal movements and habitat selection of sage grouse in southern Idaho. Pages 168–175 *in* E. D. McArthur and B. L. Welch, eds. Proc. symposium of the biology of

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

Artemisia and *Chrysothamnus*. USDA For. Serv. Gen. Tech. Rep. INT-200. 398pp.

KLEBENOW, D. A. 1972. The habitat requirements of sage grouse and the role of fire in management. Proc. Tall Timbers Tire Ecol. Conf. 12:305–315.

———. 1985. Habitat management for sage grouse in Nevada. World Pheasant Assoc. J. 10:34–46.

LEHMAN, V. W. 1941. Attwater's prairie chicken: its life history and management. U.S. Fish and Wildl. Serv. North Am. Fauna 57. 63pp.

LEOPOLD, A. S. 1977. The California quail. Univ. California Press, Berkeley. 281pp.

NELSON, O. C. 1955. A field study of the sage grouse in southeastern Oregon with special reference to reproduction and survival. M.S. Thesis, Oregon State Univ., Corvallis. 113pp.

PYRAH, D. B. 1971. Sage grouse habitat research in central Montana. Proc. West. Assoc. State Game and Fish Comm. 51:293–300.

RANDS, M. R. 1982. The influence of habitat on the population ecology of partridge. Ph.D. Thesis, Univ. Oxford, U.K. 350pp.

REDMOND, G. W., D. M. KEPPIE, AND P. W. HERZOG. 1982. Vegetative structure, concealment, and success at nests of two races of spruce grouse. Can. J. Zool. 60:670–675.

RICKARD, W. H., D. W. URESK, AND J. F. CLINE. 1975. Impact of cattle grazing on three perennial grasses in south-central Washington. J. Range Manage. 28:108–112.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Sixth ed. Iowa State Univ. Press, Ames. 507pp.

SUGDEN, L. G., AND G. W. BEYERSERGEN. 1987. Effect of nesting cover and density on American crow predation on simulated duck nests. J. Wildl. Manage. 51:481–485.

WAKKINEN, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. M.S. Thesis, Univ. Idaho, Moscow. 57pp.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movement and nesting of sage grouse hens in central Montana. J. Wildl. Manage. 38:630–633.

WINWARD, A. H. 1991. A renewed commitment to management of sagebrush grasslands. Pages 2–7 *in* Management in the sagebrush steppe. Agric. Exp. Stn. Spec. Rep. 880. Oregon State Univ., Corvallis. 48pp.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 620pp.

Received 29 July 1992.
Accepted 20 April 1993.
Associate Editor: Morrison.

This content downloaded from 204.124.92.254 on Fri, 03 Jun 2016 14:27:06 UTC
All use subject to http://about.jstor.org/terms

BioOne RESEARCH EVOLVED

A Meta-analysis of Greater Sage-grouse *Centrocercus urophasianus* Nesting and Brood-rearing Habitats

Author(s): Christian A. Hagen, John W. Connelly, Michael A. Schroeder
Source: Wildlife Biology, 13(sp1):42-50.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/0909-6396(2007)13[42:AMOGSC]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.2981/0909-6396%282007%2913%5B42%3AAMOGSC%5D2.0.CO%3B2

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats

Christian A. Hagen, John W. Connelly & Michael A. Schroeder

Hagen, C.A., Connelly, J.W. & Schroeder, M.A. 2007: A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. - Wildl. Biol. 13 (Suppl. 1): 42-50.

The distribution and range of the greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America. Although there is an unprecedented effort to conserve the species, there is still considerable debate about the vegetation composition and structure required for nesting and brood-rearing habitat. We conducted a meta-analysis of vegetation characteristics recorded in studies at nest sites (N = 24) and brood habitats (N = 8) to determine if there was an overall effect (Hedge's d) of habitat selection and to estimate average canopy cover of sagebrush *Artemisia* spp., grass and forbs, and also height of grass at nest sites and brood-rearing areas. We estimated effect sizes from the difference between use (nests and brood areas) and random sampling points for each study, and derived an overall effect size across all studies. Sagebrush cover (d_{++} = 0.39; 95% C.I.: 0.19-0.54) and grass height (d_{++} = 0.28; 95% C.I.: 0.13-0.42) were greater at nest sites than at random locations. Vegetation at brood areas had less sagebrush cover (d_{++} = -0.17; 95% C.I.: -0.44 - +0.18), significantly taller grasses (d_{++} = 0.31; 95% C.I.: 0.14-0.45), greater forb (d_{++} = 0.48; 95% C.I.: 0.30-0.67) and grass cover (d_{++} = 0.17; 95% C.I.: 0.08-0.27) than at random locations. These patterns were especially evident when we examined early (< 6 weeks post hatching) and late brood-rearing habitats separately. The overall estimates of nest and brood area vegetation variables were consistent with those provided in published guidelines for the management of greater sage-grouse.

Key words: Artemisia spp., breeding habitat, effect size, greater sage-grouse, Hedges' d, meta-analysis, sagebrush

Christian A. Hagen, Oregon Department of Fish and Wildlife, 61374 Parrell Rd, Bend, Oregon 97701, USA - e-mail: christian.a.hagen@state.or.us
John W. Connelly, Idaho Department of Fish and Game, Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA - e-mail: jcsagegrouse@aol.com
Michael A. Schroeder, Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, Washington 98813, USA - e-mail: schromas@dfw.wa.gov

Corresponding author: Christian A. Hagen

The distribution and range of greater sage-grouse *Centrocercus urophasianus* have been reduced by 56% since the European settlement of western North America (Connelly & Braun 1997, Schroeder et al. 2004). Although loss and fragmentation of sagebrush *Artemisia* spp. habitats have been cited as the primary causes for the decline of the species, degradation of existing habitat also has been con-

sidered an important factor (Braun 1998). Guidelines for protection and management of nesting and brood-rearing habitat have been provided to land managers (Connelly et al. 2000). In general, a range of 15-25% sagebrush, > 10% forb, > 15 % grass canopy cover and, a herbaceous height of 18 cm are needed for breeding habitats of greater sage-grouse.

Techniques used to measure vegetation characteristics have not always been consistent (Wamboldt et al. 2006). Additionally, some researchers and managers have questioned the applicability of management guidelines (Connelly et al. 2000) across the range of the greater sage-grouse, as well as the techniques used to derive the earlier estimates of vegetative cover and height (Bates et al. 2004, Schultz 2004). In particular, subsequent debate over the quantitative properties of the recommended vegetative characteristics required for greater sage-grouse has become a hindrance to implementing conservation actions. To address these concerns and examine the relevance of management guidelines additional analyses are needed. One potential analytical method that was not used when producing the earlier guidelines (Braun et al. 1977, Connelly et al. 2000) was the research synthesis or meta-analysis, which allows an evaluation of the generality of a given effect as a result of combining parameter estimates (effect sizes) from a set of studies (Hall et al. 1994). The use of meta-analysis can advance our knowledge and understanding of observed findings, and contribute to the advancement of more theoretical issues (Hedges & Olkin 1985).

Schultz (2004) analysed the data set in Connelly et al. (2000) and used the analysis to critique the published guidelines. However, since these articles were published, more data have become available. Because the interpretation of earlier research is a fundamental tool in the development of appropriate guidelines to management, we employed meta-analytic techniques to the research summarized by Connelly et al. (2000) as well as research conducted more recently. The purpose of our meta-analysis was to estimate the effect of habitat selection of breeding habitats (i.e. nesting and brood rearing) of greater sage-grouse. To this end we compared vegetation characteristics at use sites to random points, to evaluate the similarity of effect sizes across studies, and to determine if the overall effect size for each vegetation characteristic is statistically or biologically meaningful.

Methods

Literature review and data selection

We reviewed peer-refereed articles and graduate research theses (N = 15) and non-refereed agency reports (N = 4) that pertained to greater sage-grouse habitat use during the nesting and brood-rearing periods (Tables 1 and 2). Because studies reported significant differences in vegetation between years (Fischer 1994, Apa 1998, Sveum et al. 1998, Holloran 1999) or study areas (Gregg 1991, Drut 1992, Slater 2003) we estimated effect size for each significant unit. We included estimates from studies that reported actual cover values (e.g. 32.3%) and excluded values from one study (Klott et al. 1993) that used ranked cover values (e.g. 1-5 from Daubenmire (1959) readings). In some studies, a limited number of vegetative characteristics were recorded, thus sample sizes in Tables 1 and 2 vary for each estimate of effect size. We examined the relationship of sagebrush cover, grass cover, forb cover and grass height at nest sites and brood-use sites compared to their respective random points. These variables were consistently reported across studies and provided the largest sample sizes for our comparisons. Several articles reported only shrub cover (e.g. Drut 1992, Gregg 1993, Fischer 1994, Hanf et al. 1994, Sveum et al. 1998), which may have included a mix of sagebrush and other shrubs. Because of limited sample sizes, we estimated effect sizes and parameter estimates for sagebrush only and shrub cover (i.e. sagebrush and other shrub cover) and present results for each. Canopy cover was sometimes estimated with line-intercept or quadrats. However, because we used a standardized metric in our meta-analysis, we could compare studies that used these different methodologies (Hedges & Olkin 1985, Gurevitch & Hedges 1999). Because brood survival rates and habitat use differ between 0-6 weeks post hatching and > 6 weeks post hatching (Holloran 1999, Lyon 2000), we estimated effect sizes for brood-use by early and late periods for studies that differentiated between them. We estimated a pooled effect size for studies that did not differentiate between early and late brood-rearing periods.

Data analysis

A general equation for an effect size is the treatment mean minus control mean divided by the pooled variance (Hedges 1982). The effect size for each study serves as a dependent variable that can be modeled as a function of discrete or continuous explanatory

Table 1. Studies and vegetation data used in meta-analyses of greater sage-grouse nesting habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) or Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

		Nest site vegetation								
Study	Vegetation community	N	Shrub cover	SD	Grass cover	SD	Forb cover	SD	Grass height	SD
Aldridge 2005	SS	93	25.46	18.52	19.56	16.59	3.82	5.30	33.94	20.25
Aldridge & Brigham 2002	SS	29	31.90	21.92	31.90	21.33	8.10	6.03	30.90	19.28
Apa 1998 (1989)	MT	11	22.00	12.60	16.20	9.95	11.50	5.64	23.00	4.97
Apa 1998 (1990)	MT	10	18.80	6.32	17.00	6.01	9.00	5.06	32.40	6.01
Apa 1998 (1991)	MT	18	16.70	7.64	13.50	5.09	8.60	12.73	41.90	7.64
Fischer 1994 (Postburn)	WY	67	17.90	38.08	29.30	10.64	4.30	4.09	22.10	7.37
Fischer 1994 (Preburn)	WY	71	29.00	1.20	7.20	25.85	ND	ND	19.80	6.74
Gregg 1991(Jackass Creek)	WY	51	56.00	22.00	11.10	10.00	12.80	11.00	ND	ND
Gregg 1991 (Hart Mountain)	MT	47	51.00	15.00	18.00	20.00	6.50	5.00	ND	ND
Hanf et al. 1994	WY	20	44.00	8.90	15.00	8.94	5.00	8.94	22.00	13.42
Hausleitner 2003	MT	93	26.90	13.50	3.70	3.86	6.90	7.71	13.80	6.75
Heath et al. 1998	WY	42	19.00	12.90	8.20	4.73	2.04	2.33	16.60	3.56
Holloran 1999 (1997)	WY	32	24.90	11.80	5.50	3.53	6.70	3.64	20.80	4.25
Holloran 1999 (1998)	WY	45	25.20	9.72	4.10	1.74	7.80	3.65	17.10	2.73
Klott et al. 1993	WY	8	24.47	15.75	ND	ND	ND	ND	16.69	8.70
Lyon 2000	WY	50	25.60	991	10.60	11.70	8.20	9.21	21.30	4.25
Popham & Gutiérrez 2003	WY	40	14.50	18.97	12.50	15.81	ND	ND	23.10	18.97
Schroeder 1995	WY	78	17.24	9.76	51.03	15.94	20.64	13.35	107.88	28.62
Slater 2003 (Collett Creek)	WY	64	22.24	11.68	6.23	3.36	7.96	6.88	18.21	3.04
Slater 2003 (Salt Creek)	WY	21	24.80	8.29	3.26	2.84	1.33	1.47	16.23	3.16
Sveum et al. 1998 (1992)	WY	21	51.00	27.50	26.00	20.62	12.00	13.75	ND	ND
Sveum et al. 1998 (1993)	WY	45	59.00	26.83	27.00	20.12	21.00	20.12	ND	ND
Wakkinen 1990	WY	49	21.50	41.08	6.50	24.65	ND	ND	18.20	7.00
Wik 2002	WY	38	21.00	8.63	58.00	17.88	ND	ND	25.00	7.40

variables or used to estimate a cumulative effect size. The effect size magnitude can be ranked small (0.2), medium (0.5) or large (0.8) standard deviations from a null effect size of zero, as a general rule (Cohen 1969).

We used Hedges' d (Hedges 1982) to estimate effect sizes for sagebrush cover, grass height, grass cover and forb cover for each study because it is conducive to estimating an effect between paired treatments. With E as the treatment group and C as the control, Hedges' d was calculated as:

$$d = \frac{\bar{X}^E - \bar{X}^c}{S} J$$

where S is the pooled standard deviation and the variance ($v = \sqrt{S}$) of Hedges' d is:

$$v = \frac{N^c + N^E}{N^c N^E} + \frac{d^2}{2(N^c + N^E)}$$

and J is the correction for small sample sizes:

$$J = 1 - \frac{3}{4(N^c + N^E - 2) - 1}$$

We estimated cumulative effect size d_{++} as:

$$d_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where the weight w_i for study i is the reciprocal of the variance ($w_i = 1/v$). We used random sites as the 'control' group and use (nests or brood) sites as the 'treatment' group; thus, a positive estimate of d indicates that the variable was greater at use sites than at random points. Confidence limits (95% C.I.) were

Table 2. Studies and vegetation data used in the meta-analyses of greater sage-grouse brood-rearing habitats throughout North America. Sagebrush (shrub), grass and forb canopy cover (in %) and grass height (in cm) were vegetation variables considered in the analyses. Dominant vegetation community was described in each study as silver sagebrush (SS), mountain big sagebrush (MT) and Wyoming big sagebrush (WY). ND means that no data were available or had been reported in a manner that was usable in the meta-analysis.

	Brood-rearing area vegetation									
Brood period/study	Vegetation community	N	Shrub cover	SD	Grass cover	SD	Forb cover	SD	Grass height	SD
Early										
Drut 1992 (Hart Mt)	MT	87	23.00	8.00	15.00	7.00	11.00	7.00	ND	ND
Drut 1992 (Jackass)	WY	84	26.00	8.00	9.00	5.00	13.00	6.00	ND	ND
Hausleitner 2003	MT	31	12.70	10.02	5.80	2.78	7.50	3.90	21.70	5.57
Heath et al. 1998	WY	16	14.40	8.80	12.50	13.20	2.80	2.80	16.10	4.80
Holloran 1999	WY	67	15.83	8.67	5.89	5.74	9.25	4.93	18.59	4.94
Lyon 2000	WY	23	21.50	7.35	14.20	18.10	8.30	9.91	23.30	4.90
Sveum 1995	WY	53	11.00	7.28	17.00	21.84	22.00	14.56	ND	ND
Late										
Drut 1992 (Hart Mt)	MT	38	24.00	9.50	16.00	7.00	20.00	8.00	ND	ND
Drut 1992 (Jackass)	WY	38	29.00	15.00	8.00	5.00	8.00	6.00	ND	ND
Hausleitner 2003	MT	28	8.40	7.41	9.10	9.52	8.90	5.29	20.00	5.82
Heath et al. 1998	WY	22	11.10	10.79	15.60	19.23	10.10	11.73	15.60	6.10
Holloran 1999	WY	59	17.40	12.10	5.26	2.83	9.01	5.17	16.53	4.35
Sveum 1995	WY	19	7.00	8.72	18.00	13.08	23.00	13.08	ND	ND
Both										
Aldridge 2005	SS	139	8.85	7.90	21.20	13.56	8.88	9.08	8.85	7.90
Aldridge & Brigham 2002	SS	91	20.90	15.55	34.20	19.56	10.90	11.45	20.90	15.55
Apa 1998	MT	49	14.10	11.90	10.00	9.80	8.00	11.20	14.10	11.90
Klott et al. 1993	WY	13	16.76	5.72	ND	ND	ND	ND	10.60	11.51
Hausleitner 2003	MT	92	10.60	11.51	6.50	5.75	8.00	6.71	16.48	4.21
Slater 2003	WY	13	13.50	13.41	6.81	5.77	5.45	6.20	13.50	13.41
Wik 2002	WY	46	15.00	10.17	50.00	14.24	16.00	10.17	20.00	6.78

estimated for d, and we used bias-corrected bootstrap sampling to estimate confidence limits for d_{++}, to account for replicate years or areas within studies. We evaluated the plausibility of using additional explanatory variables to explain the observed differences in effect sizes across studies. The Q_T statistic is based on the total sum of squares and specifically tests for equal effect sizes across studies. If Q_T is greater than would be expected at random (χ^2-distribution), then additional variables (e.g. nest success rates) might help explain the observed variation in the data. We assumed that random variation occurred across nesting studies and estimated effect sizes using random effects models (Hedges 1982). However, we used mixed models to identify if there was a common effect size across brood-rearing periods (categorical data) for each cover type. The basic assumption for this analysis is that random variation occurs among effect sizes within a brood period, but may differ between periods (Gurevitch & Hedges 1999). Here the statistic Q_B can be used to assess the amount of variation accounted for between groups. If Q_B is significantly large, it suggests that effect sizes are larger between groups than expected from random. Applications of mixed-model meta-analysis are uncommon in ecological studies, but likely are the most appropriate for such data sets (Gurevitch & Hedges 1999). All meta-analytic calculations were conducted in MetaWin 2.0 (Rosenberg et al. 2000).

The quality of a research synthesis hinges on the quality of the publications available to analyse, as well as on studies not published because of a lack of significant results (Rosenberg 2005). This is referred to as publication bias and can overestimate the effect size if a large number of non-significant studies are not published or accessible. One of the simplest methods to evaluate the potential impact of publication bias is the calculation of a fail-safe number (N_+). A fail-safe number indicates the number of non-significant, unpublished (or missing) studies that would need to be added to a meta-analysis to reduce an overall statistically significant observed result to non-significance (Rosenberg 2005). We estimated fail-safe numbers for each significant effect size using Fail-Safe Number Calculator (Rosenberg 2005), and considered an effect size robust if $N_+ > 5N + 10$, where N is the observed number of studies used to estimate the effect size.

To add biological relevance to the meta-analysis, we used a weighted general linear model (PROC GLM; SAS Institute 2000) and estimated the mean and 95% C.I. for sagebrush cover, grass cover, forb cover and grass height at nest and brood-use sites.

Results

Effect sizes

Greater sage-grouse females selected nest sites with generally more sagebrush cover (d_{++} = 0.39; 95% C.I.: 0.19-0.54) and taller grass height (d_{++} = 0.28; 95% C.I.: 0.15-0.41) than random sites (Fig. 1). Grass (d_{++} = 0.13; 95% C.I.: -0.03 - +0.25) and forb cover (d_{++} = 0.15; 95% C.I.: -0.06 - +0.37) were greater at nest sites, but neither effect was significantly large. An examination of Q_T indicated that d was homogenous ($P > 0.2$) among studies for each variable and that additional information would not explain the observed effect sizes (Table 3). Shrub cover had a larger effect size than sagebrush only (d_{++} = 0.74; 95% C.I.: 0.39-1.13).

Vegetation at brood areas combined among all periods had greater forb cover (d_{++} = 0.46; 95% C.I.: 0.30-0.66), grass cover (d_{++} = 0.19; 95% C.I.: 0.09-0.30), significantly taller grasses (d_{++} = 0.29; 95% C.I.: 0.13-0.42), and less sagebrush cover (d_{++} = -0.17; 95% C.I.: -0.44 - +0.18) than random locations (see Fig. 1). However, females exhibited some variation in habitat selection for sagebrush between these periods (Q_B = 6.12, df = 2, P = 0.046). Generally, early brood-use areas were comprised of greater forb cover (d_{++} = 0.57; 95% C.I.: 0.23-0.80), grass cover (d_{++} = 0.27; 95% C.I.: 0.11-0.50), and taller grass (d_{++} = 0.39; 95% C.I.: 0.26-0.60), but less sagebrush cover (d_{++} = -0.46; 95% C.I.: -0.75 - -0.19) than random sites. Effect size for shrub cover changed moderately when using all studies (d_{++} = -0.61; 95% C.I.: -0.95 - -0.31). During late brood rearing, forb cover (d_{++} = 0.55; 95% C.I.: 0.23-0.79) and grass cover (d_{++} = 0.16; 95% C.I.: 0.05-0.30) were greater at use sites, but sagebrush cover (d_{++} = -0.08; 95% C.I.: -0.48 - +0.12) and shrub cover (d_{++} = -0.04; 95% C.I.: -0.31 - +0.15) were similar between use and random sites. For studies that pooled estimates across both periods, forb cover was greater (d_{++} = 0.27; 95% C.I.: 0.04-0.54) and grass height taller (d_{++} = 0.34; 95% C.I.: 0.20-0.48) than at random sites. Sagebrush cover (d_{++} = 0.15; 95% C.I.: -0.36 - +0.77) and grass cover (d_{++} = 0.11; 95% C.I.: -0.01 - +0.32) were greater at brood use areas but neither of these factors was significant. Examination of Q_T values indicated that effect sizes were homogenous ($P > 0.25$) except for shrub cover, and additional explanatory variables would not explain variation in effect sizes across all studies (see Table 3). The test of heterogeneity is conservative with small sample sizes and therefore interpreted in an appropriately conservative manner.

Publication bias

We conducted fail-safe calculations for 12 effect sizes that were significant (see Table 3). The effect size of disproportional use of sagebrush and grass height was robust for nest sites as was forb cover at early and late brood-rearing areas (see Table 3). Grass cover and height effect sizes for brood-rearing areas were not

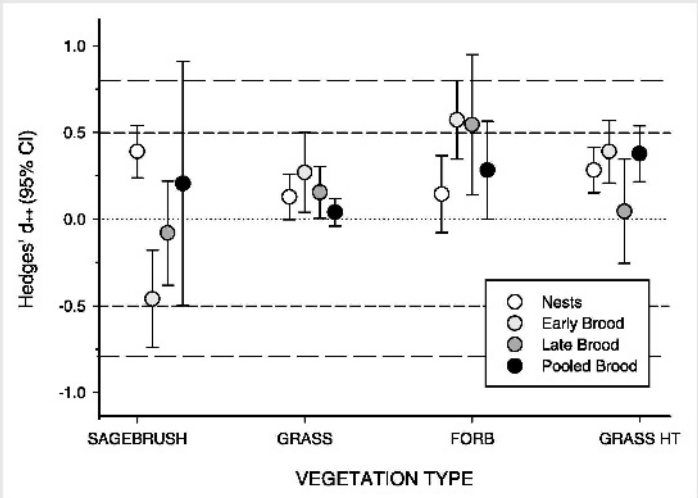


Figure 1. Cumulative effect sizes (d_{++}) by vegetation types and across nesting and brood-rearing habitats. Long-dashed lines indicate large ($d > 0.8$), small-dashed lines indicate medium ($0.8 \geq d > 0.5$), and dotted line indicates small ($0 < d < 0.5$) effects. Significant positive and negative effects indicate selection for or against a vegetation type, respectively. Estimates with 95% C.I. including 0, indicate no effect of habitat selection.

Table 3. Estimates of vegetation characteristics at greater sage-grouse use sites from 19 studies across the species range, and diagnostic statistics (Q_T, N_+) for meta-analysis. Means and confidence intervals were derived from a weighted mean linear model where the inverse of the variance was the weighting factor. The 'early' period was defined as brood habitat used < 6 weeks post hatching, the 'late' period as > 6 weeks post hatching, and 'both' were studies that pooled estimates across both periods. An asterisk (*) indicates that a fail-safe number (N_+) is robust (> 5N + 10). The fail-safe number is equivalent to the number of studies of null effect and mean weight necessary to reduce the observed significance level to $\alpha = 0.05$.

			Parameter estimates		Diagnostics			
Cover type	Period	N	$\bar{x}$	95% C.I.	Q_T	df	P	Fail safe (N_+)
Forb (%)	Nest	19	4.02	2.05-5.99	21.3	18	0.27	NA
	Early	7	6.74	3.91-9.56	4.5	6	0.61	94*
	Late	6	10.78	6.50-15.06	5.3	5	0.38	49*
	Both	6	8.51	2.92-14.10	4.4	5	0.50	13
Grass (%)	Nest	23	6.75	4.53-8.98	25.9	22	0.26	NA
	Early	7	7.56	4.35-10.76	7.5	6	0.28	14
	Late	6	7.57	4.17-10.98	3.6	5	0.61	1
	Both	6	11.44	5.79-17.10	5.4	5	0.38	NA
Sagebrush (%)	Nest	19	21.51	19.91-23.93	13.7	16	0.62	270*
	Early	4	16.84	9.59-24.08	3.2	3	0.37	14
	Late	3	10.92	1.67-20.16	1.9	2	0.38	NA
	Both	7	14.15	8.39-19.92	5.1	6	0.53	NA
Shrub cover (%)	Nest	24	25.13	20.35-29.91	35.3	23	0.05	1133*
	Early	7	18.07	13.31-22.83	5.3	6	0.50	204*
	Late	6	13.71	7.53-19.88	5.3	5	0.38	NA
Grass height (cm)	Nest	20	19.77	17.36-22.18	16.6	19	0.61	193*
	Early	4	19.78	15.91-23.65	2.8	3	0.41	5
	Late	3	17.24	12.58-21.90	1.6	2	0.45	NA
	Both	7	19.16	15.17-23.15	7.5	6	0.28	40

robust for missing studies. However, these were relatively small effect sizes (see Fig. 1). The effect size of sagebrush cover at brood-rearing areas was robust.

Parameter estimates

Sagebrush canopy cover was apparently greater at nest sites (21.5%) than at brood areas (< 16.9%; see Table 3). Combined forb (4.1%) and grass cover (6.5%) was less at nest sites than at brood areas (forb > 6.7%, grass > 7.6%). However, grass height was comparable (~19 cm) in nest and brood areas. During brood rearing, sagebrush cover decreased from early to late periods, forb cover increased, whereas grass cover and height did not change appreciably (see Table 3).

Discussion

Our study provides the first quantitative assessment of available data for greater sage-grouse habitat selection during the nesting and brood-rearing periods. We found a general effect for habitat selection across the range of these studies, as evidenced by low levels of variation in effect sizes across studies and regions. Many of our estimated effect sizes were robust to the potential impacts of publication bias, lending considerable support to the generality of our findings. There was a medium to large effect (d = 0.37-0.74) of selection for vegetation characteristics, with greater sagebrush cover for nest concealment and forb cover for females with broods. There were smaller effects (d ~ 0.2) for selection of grass height and cover by nesting and brood-rearing females. The variation of effect sizes in sagebrush cover was more substantial between brood periods, signifying a seasonal shift in habitat use.

Effect sizes

Because random variation was as expected, we can infer that greater sage-grouse females were selecting for similar nesting vegetation (greater sagebrush cover, grass cover and/or taller grasses) throughout the geographic range of these studies. This quantitative assessment supports earlier qualitative reviews of sage-grouse habitat requirements during the nesting period (Braun et al. 1977, Connelly et al. 2000) that suggested the importance of sagebrush and grass cover as well as grass height. Our study also indicated the importance of reporting sagebrush cover separately from other shrub species as there was a moderate

change in effect size and increase in variance of effect size, when comparing studies reporting sagebrush versus shrub cover. Although the measurement of grass height has only recently been standardized (Connelly et al. 2003), we identified an overall selection for taller grasses at nest sites. Additionally, the relatively small selection effect of greater grass cover may have been confounded with grass height. Many short stature grasses may have been included in the estimates of grass cover, and may contribute to the relatively small effect size of grass cover at use sites.

Brood females selected early and late habitats with less sagebrush cover and greater herbaceous cover (grass and forbs) than random sites. This generalized effect for greater herbaceous cover during brood rearing is likely a result of mesic plant communities with an abundance of invertebrates and foods that are critical to the growth and development of chicks (Johnson & Boyce 1991, Drut et al. 1994). Alternatively, this effect may have been correlated with broods seeking habitats with less shrub cover and greater understory in more xeric sites. Taller grasses were selected more so during early brood rearing than during late brood rearing. The proximity of early brood rearing to nesting sites may have contributed to this result, or because females were selecting sites with less sagebrush cover, the use of taller grasses may have provided greater vertical screening and protection. However, as broods mature tall stature grasses appeared to become less important, as did sagebrush cover. For studies that pooled vegetation measurements across both brood periods the effect sizes were generally small and may have been confounded by potential effects between early and late broods. Sagebrush cover was greater at brood use sites for pooled studies and was likely due to selection for silver sagebrush *A. cana* sites in Alberta where the extent of sagebrush could be a limiting factor (Aldridge & Brigham 2002, Aldridge 2005).

Publication bias

Generally, our findings were robust to publication bias with respect to vegetation needs for each life stage. Our evaluation of potential impacts of publication bias indicated that habitat usage by greater sage-grouse at nest sites was robust for sagebrush cover and grass height, each effect requiring two to several hundred studies of 'no effect' to nullify our results. Similarly, our estimated effects of less shrub cover and greater forb cover during brood rearing were robust to publication bias. The effects of grass cover were relatively small and more susceptible to non-significant or missing studies. These findings may help guide future work to identify vegetation characteristics that should be evaluated more carefully and perhaps reduce some of this ambiguity (e.g. grass cover).

Parameter estimates

The weighted average of cover and height values were within the range specified by the greater sage-grouse management guidelines for breeding habitats (Connelly et al. 2000). Our analysis indicated that the range (95% C.I.s) of vegetation measurements encompassed those in the guidelines published by Connelly et al. (2000), recommending 15-25% sagebrush cover, $>$ 10% forb cover, $>$ 15% grass cover and $\geq$ 18-cm grass height (see Table 3). Estimates of sagebrush were not markedly different when we included studies that reported only shrub cover. Despite criticisms of the established guidelines (Bates et al. 2004, Schultz 2004), our quantitative analysis that includes new data published after 2000 strongly suggests that these values for describing breeding habitats are reasonable. Because these measurements are generally recorded over relatively small scales ($<$ 30 m), identifying the appropriate proportions of these vegetative characteristics in a larger landscape is paramount (Bates et al. 2004).

Conclusions and recommendations

The magnitude of effects sizes combined with the parameter estimates in our meta-analyses demonstrated a shift in habitat selection by females between nesting and brood-rearing periods, primarily a shift in sagebrush and forb canopy cover. However, most studies have not quantified the spatial distribution or juxtaposition of these vegetative communities. Understanding the optimum mix and spatial arrangement of these communities and their effects on demographic rates in a landscape could substantially enhance management of the greater sage-grouse. More importantly, studies of breeding habitats need to begin to examine the relationship between vegetative communities, landscape metrics (e.g. habitat patch size, fragmentation and distance to roads) and demographic rates. Similarly, as more studies begin to compare vegetation and other differences between successful and unsuccessful nests, a meta-analysis could prove useful in identifying a general effect for factors contributing to nest success.

Acknowledgements - many biologists and ecologists from state and federal natural resources agencies provided useful

insight and encouraged us to write this paper. We appreciate their support. We thank the Oregon Department of Fish and Wildlife, Idaho Department of Fish and Game, and Washington Department of Fish and Wildlife for supporting our efforts in this work. This is a contribution from Idaho Federal Aid in Wildlife Restoration Project W-160-R and Washington Federal Aid in Wildlife Restoration. M.J. Holloran, L. Ellison and three anonymous reviewers provided comments that greatly enhanced the quality of this manuscript.

References

Aldridge, C.L. 2005: Identifying habitats for persistence of greater sage-grouse (Centrocercus urophasianus) in Alberta, Canada. - PhD thesis, University of Alberta, Edmonton, Canada, 250 pp.

Aldridge, C.L. & Brigham, R.M. 2002: Sage-grouse nesting and brood habitat use in southern Canada. - Journal of Wildlife Management 66: 433-444.

Apa, A.D. 1998: Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA, 199 pp.

Bates, J., Davies, K. & Miller, R. 2004: Ecology of the Wyoming big sagebrush alliance in the northern Great Basin: 2004 Progress Report. - Eastern Oregon Agricultural Research Center, Burns, Oregon, USA, 65 pp.

Braun, C.E. 1998: Sage grouse declines in western North America: what are the problems? - Transactions of Western Association of Fish and Wildlife Agencies 78: 139-156.

Braun, C.E., Britt, T. & Wallestad, R.O. 1977: Guidelines for maintenance of sage grouse habitats. - Wildlife Society Bulletin 5: 99-106.

Cohen, J. 1969: Statistical power analysis for the behavioral sciences. - Erlbaum, Hillsdale, New Jersey, USA, 567 pp.

Connelly, J.W. & Braun, C.E. 1997: Long-term changes in sage grouse Centrocercus urophasianus populations in western North America. - Wildlife Biology 3: 229-234.

Connelly, J.W., Schroeder, M.A., Sands, A.R. & Braun, C.E. 2000: Guidelines to manage sage grouse populations and their habitats. - Wildlife Society Bulletin 28: 967-985.

Connelly, J.W., Reese, K.P. & Schroeder, M.A. 2003: Monitoring of greater sage-grouse habitats and populations. - College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, USA, 50 pp.

Daubenmire, R. 1959: A canopy-coverage method of vegetational analysis. - Northwest Science 33: 43-64.

Drut, M.S. 1992: Habitat use and selection by sage grouse broods in southeastern Oregon. - M.Sc. thesis, Oregon State University, Corvallis, USA, 44 pp.

Drut, M.S., Crawford, J.A. & Gregg, M.A. 1994: Brood habitat use by sage grouse in Oregon. - Great Basin Naturalist 54: 170-176.

Fischer, R.A. 1994: The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA, 150 pp.

Gregg, M.A. 1991: Use and selection of nesting habitat by sage grouse in Oregon. - M.Sc. thesis, Oregon State University, Corvallis, USA, 46 pp.

Gurevitch, J. & Hedges, L.V. 1999: Statistical issues in ecological meta-analyses. - Ecology 80: 1142-1149.

Hall, J.A., Rosenthal, R., Tickle-Degnen, L. & Mosteller, F. 1994: Hypotheses and problems in research synthesis. - In: Cooper, H. & Hedges, L.V. (Eds.); The Handbook of research synthesis. Russell Sage Foundation, New York, USA, pp. 17-28.

Hanf, J.M., Schmidt, P.A. & Groshens, E.B. 1994: Sage grouse in the high desert of central Oregon: results of a study, 1988-1993. - Bureau of Land Management, Portland, Oregon, USA, 67 pp.

Hausleitner, D. 2003: Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. - M.Sc. thesis, University of Idaho, Moscow, USA, 162 pp.

Heath, B.J., Straw, R., Anderson, S.H., Lawson, J. & Holloran, M.J. 1998: Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different livestock grazing, predator control, and harvest management practices. - Project Completion Report, Wyoming Game and Fish Department, Cheyenne, USA, 71 pp.

Hedges, L.V. 1982: Estimation of effect size from a series of independent experiments. - Psychological Bulletin 92: 490-499.

Hedges, L.V. & Olkin, I. 1985: Statistical methods for meta-analysis. - Academic Press, San Diego, California, USA, 369 pp.

Holloran, M.J. 1999: Sage grouse (Centrocercus urophasianus) seasonal habitat use near Casper, Wyoming . - M.Sc. thesis, University of Wyoming, Laramie, USA, 123 pp.

Johnson, G.D. & Boyce, M.S. 1991: Survival, growth, and reproduction of captive-reared sage grouse. - Wildlife Society Bulletin 19: 88-93.

Klott, J.H., Smith, R.B. & Vullo, C. 1993: Sage grouse habitat use in the Brown's Bench area of south-central Idaho. - United States Department of Interior, Bureau of Land Management, Idaho State Office, Technical Bulletin 93-4, Boise, Idaho, USA, 14 pp.

Lyon, A.G. 2000: The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA, 121 pp.

Popham, G.P. & Gutiérrez, R.J. 2003: Greater sage-grouse Centrocercus urophasianus nesting success and habitat use in northeastern California. - Wildlife Biology 9: 327-334.

Rosenberg, M.S. 2005: The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. - Evolution 59: 464-468.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. 2000: Metawin: statistical software for Meta-analysis Version 2.0. - Sinauer Associates, Sunderland, Massachusetts, USA, 128 pp.

SAS Institute 2000: SAT/STAT user's guide, Release 8.0 Edition. - SAS Institute, Inc. Cary, North Carolina, USA. Available at: http://v8doc.sas.com/sashtml/

Schroeder, M.A. 1995: Productivity and habitat use of sage grouse in north-central Washington. Job Progress Report W-96-R. -Washington Department of Fish and Wildlife, Olympia, USA, 23 pp.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Diebert, P., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V. & Stiver, S.J. 2004: Distribution of sage-grouse in North America. - Condor 106: 363-376.

Schultz, B. 2004: Analysis of studies used to develop herbaceous height and cover guidelines for sage grouse nesting habitat. - Cooperative Extension Special Publication SP-04-11, University of Nevada, Reno, USA, 25 pp.

Slater, S.J. 2003: Sage-grouse (Centrocercus urophasianus) use of different-aged burns and the effects of coyote control in southwestern Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA, 177 pp.

Sveum, C.M. 1995: Habitat selection by sage-grouse hens during the breeding season in south-central Washington. - M.Sc. thesis, Oregon State University, Corvallis, USA, 86 pp.

Sveum, C.M., Edge, W.D. & Crawford, J.A. 1998: Nesting habitat selection by sage grouse in south-central Washington. - Journal of Range Management 51: 265-269.

Wakkinen, W.L. 1990: Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. - M.Sc. thesis, University of Idaho, Moscow, USA, 57 pp.

Wambolt, C.L., Frisina, M.R., Knapp, S.J. & Frisina, R.M. 2006: Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. - Wildlife Society Bulletin 34: 440-445.

Wik, P.A. 2002: Ecology of greater sage-grouse in south-central Owyhee County, Idaho. - M.Sc. thesis, University of Idaho, Moscow, USA, 141 pp.

BioOne RESEARCH EVOLVED

Nesting Ecology of Greater Sage-Grouse *Centrocercus urophasianus* at the Eastern Edge of their Historic Distribution

Author(s): Katie M. Herman-Brunson, Kent C. Jensen, Nicholas W. Kaczor, Christopher C. Swanson, Mark A. Rumble & Robert W. Klaver
Source: Wildlife Biology, 15(4):395-404.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/09-005
URL: http://www.bioone.org/doi/full/10.2981/09-005

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Wildl. Biol. 15: 395-404 (2009)
DOI: 10.2981/09-005
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution

Katie M. Herman-Brunson, Kent C. Jensen, Nicholas W. Kaczor, Christopher C. Swanson, Mark A. Rumble & Robert W. Klaver

Greater sage-grouse *Centrocercus urophasianus* populations in North Dakota declined approximately 67% between 1965 and 2003, and the species is listed as a Priority Level 1 Species of Special Concern by the North Dakota Game and Fish Department. The habitat and ecology of the species at the eastern edge of its historical range is largely unknown. We investigated nest site selection by greater sage-grouse and nest survival in North Dakota during 2005 - 2006. Sage-grouse selected nest sites in sagebrush *Artemisia* spp. with more total vegetative cover, greater sagebrush density, and greater 1-m visual obstruction from the nest than at random sites. Height of grass and shrub (sagebrush) at nest sites were shorter than at random sites, because areas where sagebrush was common were sites in low seral condition or dense clay or clay-pan soils with low productivity. Constant survival estimates of incubated nests were 33% in 2005 and 30% in 2006. Variables that described the resource selection function for nests were not those that modeled nest survival. Nest survival was positively influenced by percentage of shrub (sagebrush) cover and grass height. Daily nest survival decreased substantially when percentage of shrub cover declined below about 9% and when grass heights were less than about 16 cm. Daily nest survival rates decreased with increased daily precipitation.

Key words: Centrocercus urophasianus, eastern range, edge of distribution, habitat, nesting, sage-grouse

Katie M. Herman-Brunson, Kent C. Jensen, Nicholas W. Kaczor** & Christopher C. Swanson, Department of Wildlife and Fisheries Sciences, SPB 138D, P.O. Box 2140B, South Dakota State University, Brookings, South Dakota, 57007, USA - e-mail addresses: kherman20@hotmail.com (Katie M. Herman-Brunson); Kent.Jensen@sdstate.edu (Kent C. Jensen); Nicholas_Kaczor@blm.gov (Nicholas W. Kaczor); christopher.swanson@sdstate.edu (Christopher C. Swanson)*
Mark A. Rumble, U.S. Forest Service Rocky Mountain Research Station, 8221 S. Highway 16, Rapid City, South Dakota, 57702, USA - e-mail: mrumble@fs.fed.us
Robert W. Klaver, Earth Resources Observation and Science Center, U.S. Geological Survey, 47914 252nd Street, Sioux Falls, South Dakota, 57198, USA - e-mail: bklaver@usgs.gov

Present addresses:
**Campbell County School District, Meadowlark Elementary School, 816 E 7th Street, Gillette Wyoming 82718, USA,*
***U.S. Bureau of Land Management, 280 Hwy 191 N, Rock Springs , Wyoming 82901, USA*

Corresponding author: Mark A. Rumble

Received 10 January 2009, accepted 13 May 2009

Associate Editor: Ilse Storch

Greater sage-grouse *Centrocercus urophasianus* populations have declined by 45-80% across their range (Schroeder et al. 2004, Connelly et al. 2004). In North Dakota, greater sage-grouse (hereafter sage-grouse) declined approximately 67% from 1965 to 2003 (Connelly et al. 2004). While sage-grouse in North Dakota are genetically contiguous with populations in Montana and South Dakota (Oyler-McCance et al. 2005), they could become isolated by conversion of sagebrush into agriculture (Smith et

al. 2005), and oil and gas development (Connelly et al. 2004, Walker et al. 2007). Long-term population declines in sage-grouse in North Dakota (Smith et al. 2005) have resulted in classifying sage-grouse as Priority Level 1 Species of Special Concern in North Dakota (McCarthy & Kobriger 2005). Altered habitat quality and quantity in sagebrush ecosystems (e.g. Connelly et al. 2004, Welch 2005) may result in low survival and productivity of sage-grouse (Aldridge & Brigham 2001), and declining populations. Therefore, understanding characteristics important to selection of nest sites and factors that affect nest survival is critical to the management, conservation and rehabilitation of sagebrush habitats for sage-grouse. Despite well-understood reproductive ecology in the core of the sage-grouse range, knowledge of reproductive ecology and habitat selection by sage-grouse occurring at the eastern edge of their distribution is limited. Therefore, our objective was to quantify nest habitat selection by sage-grouse in North Dakota and determine specific factors associated with survival of sage-grouse nests. These data will help in the development of management recommendations to assist state and federal agencies in managing habitats for sage-grouse.

Material and methods

Study area

Our study area included the counties of Bowman and Slope in southwestern North Dakota and Fallon in southeastern Montana. The area has flat to gently-rolling prairie, with a few buttes and intermittent streams. Annual precipitation ranges from 35.6 cm to 40.6 cm, most of which occurs during April - September. Summer temperatures range from 9.9°C to 27.5°C, and winter temperatures range from -15.6°C to 0.2°C (North Dakota Agricultural Weather Network 2006).

Vegetation communities included mixed grass prairie with perennial and annual forbs and grasses and shrub steppe comprised of silver sagebrush *Artemisia cana*, Wyoming big sagebrush *A. tridentata wyomingensis*, rubber rabbitbrush *Chrysothamnus nauseosus* and greasewood *Sarcobatus vermiculatus*. Common grasses included western wheatgrass *Pascopyrum smithii*, Kentucky bluegrass *Poa pratensis*, Japanese brome *Bromus japonicus*, needle and thread *Stipa comata* and junegrass *Koeleria macrantha*. Forbs included common dandelion *Taraxacum officinale*, common yarrow *Achillea millefodium* and textile onion *Allium textile* (Johnson & Larson 1999).

Most of the land is privately owned, and the primary land use is cattle ranching. Areas managed by the Bureau of Land Management (BLM) for grazing were stocked at 4-10 acres per animal unit month (AUM) under continuous or rotational grazing that begins in early to mid June (Mitch Iverson, Belle Fourche BLM, pers. comm.). Oil and gas development is extensive in some areas.

Capture and telemetry

We captured female sage-grouse at night on or near leks from late March through April in 2005 and 2006 (Wakkinen et al. 1992b). We recorded age (Crunden 1963) and placed a 20-g necklace radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota) with mortality sensors on each female. The transmitters were $<2\%$ of the body weight of individually marked sage-grouse. All field methods complied with the Institutional Animal Care and Use Committee (07-A032) at South Dakota State University.

We located females 2-3 times each week from the time they were captured and radio-marked, until the outcome of nesting had been determined aided with a hand-held 3-element yagi antenna. Nests were inconspicuously marked with plastic flagging >20 m south of the nest, near or at ground level to avoid making them visible except on close inspection. The nest location was recorded with a GPS. Occasionally, the interval between telemetry locations was greater than 2-3 days, because weather prohibited access to the nest area. Therefore, onset of incubation could not be accurately estimated from the behaviour of females. As a result, we flushed incubating hens and estimated nest initiation by backdating from incubation stage estimated from egg flotation (Hays & LeCroy 1971) and adding 1.3 days for each egg laid (Patterson 1952). If the female was absent from the nest area for >3 consecutive locations, we approached the nest site to determine fate. Success or failure of nests was determined by membrane conditions of the eggs (Klebenow 1969) or observation of a brood with the radio-collared female. Nests were considered successful if ≥ 1 egg hatched.

Vegetation measurements

During May - June each year of the study, we characterized vegetation at nest sites and random sites. Most sage-grouse nest within 3.2 km of a lek (Braun

et al. 1977, Aldridge & Brigham 2001), so we selected random sites from which to estimate resource selection for nesting from within a 3-km buffer surrounding leks on which we observed sage-grouse. Because nest sites are normally located beneath sagebrush (Connelly et al. 2000), we selected random sites at the nearest sagebrush plant to the random coordinates. We recorded slope and aspect at each nest and random site using a clinometer and compass.

We established four 50-m long transects that were centered over the nest or random site. We recorded species, height, length and width of sagebrush plants at the intersection of these transects. Using 10-m intervals (N = 20) along each transect, we recorded the distance to the nearest shrub (usually sagebrush) using a point-centered-quarter method (Cottam & Curtis 1956), and recorded the species, height, length and width of each shrub. We also recorded the maximum height of grass growing from beneath the sagebrush. We estimated visual obstruction (VOR) and height of grass at each nest site, and for each meter out to five meters from the nest, and then at 10-m intervals along each transect using a modified Robel pole delineated in 2.54-cm increments (Robel et al. 1970, Benkobi et al. 2000). We used the Daubenmire (1959) method to estimate canopy cover of vegetation. This method is amenable to collecting data on windy days and yields data that are similar (< 3% difference for sagebrush) to the line-intercept method (Floyd & Anderson 1987), and may provide more accurate estimates than line-intercept methods (Booth et al. 2006). We estimated canopy cover from a height of about 1 m in 24 0.1-m^2 quadrats (Daubenmire 1959). Four quadrats were placed at the intersection of the transects (over the nest) and at the four terminal ends of 1-m legs forming the pattern of an H every 10 m along each transect. We estimated percentage of canopy cover for total cover, total shrubs, total forbs, total grasses, litter, bare ground, sagebrush and dominant species of grasses and forbs using six categories (Daubenmire 1959). We obtained measures of maximum and minimum daily temperature and daily precipitation throughout the nesting season from the closest weather station in Bowman County (North Dakota Agricultural Weather Network 2006).

Data analyses

Nesting

We tested for differences in clutch size distributions between adults and yearlings using χ^2 goodness of fit test. χ^2 goodness of fit tests were used to test differences in nest initiation rates between years and among ages of females. We calculated distance from each nest to the center of nearest lek and distance from each nest to lek of capture (if the hen was captured that year) using corresponding GPS coordinates. We tested for differences in these distributions between successful and unsuccessful nests, and between adults and yearling hens using a multiple response permutation program (MRPP; Mielke & Berry 2001). Statistical significance was determined at $\alpha \leq 0.05$ for these tests.

Habitat selection

Average percentage of canopy cover was recorded for each variable at nests and random sites. We calculated VOR at the nest and at 1-m intervals out to five meters. Average VOR was also calculated for each site. We estimated sagebrush density using maximum likelihood estimates of point-centered-quarter method (Pollard 1971). We then used MRPP to test the distribution of vegetation characteristics between nests and random sites to distinguish important variables to include in models of nest survival and selection of nest sites. Statistical significance was determined with a critical value of $\alpha \leq 0.05$.

We used an information theoretic approach (Burnham & Anderson 2002) with logistic regression to estimate models depicting vegetation characteristics selected by female sage-grouse for nests. Because we had a very large number of variables from estimated canopy cover by species and collected extensive measurements, we developed 10 candidate models that included variables that exhibited differences between nest and random sites from MRPP tests (see Hosmer & Lemeshow 2000, Guthery et al. 2005, Stephens et al. 2005). These models included percent total cover, percent grass cover, percent forb cover, percent sagebrush cover and sagebrush height, site-VOR, nest VOR, 1-m VOR, grass height from the Robel pole and sagebrush density. Year was considered a design variable and was included in all candidate models. We tested the strength of the best predictive model of nest sites selected using receiver operating characteristic curves (ROC). ROC values between 0.8 and 0.9 were considered excellent discrimination, and ROC values between 0.7 and 0.8 were considered acceptable discrimination (Hosmer & Lemeshow 2000). The statistical tests described above were made using SPSS (2002) or SAS (2005).

Nest survival

We estimated daily survival rate (DSR) of nests using the nest survival model in Program MARK (White & Burnham 1999, Dinsmore et al. 2002). We established 6 May as first nest day.

Nest survival probabilities were estimated as a function of age of hen, nest age and vegetation characteristics at nests. We then modeled effects of the time-dependent variables year, maximum and minimum daily temperature, and daily precipitation using the best survival models from the previous analysis also using program MARK (White & Burnham 1999). Continuous covariates were standardized as deviations from a mean of 0. Categorical and time-dependent covariates were coded with the actual values so they would not hamper numerical optimization of likelihood (Burnham & Anderson 2002).

Results

We captured and fitted 30 hens with necklace-mounted radio-transmitters during spring 2005-2006 (21 during 2005 and 9 during 2006); 36% were adults. Of the hens captured in 2005, 11 survived and were included in our sample in 2006.

Nesting

Adults initiated nests approximately five days earlier than yearlings. Nests were 6-8 days on average into incubation when detected. There were two renests in 2005 which were initiated in mid- to late May; no renesting occurred in 2006. The renesting rate was 10%. All radio-collared hens initiated a nest in 2005. In 2006, 13 of 14 adults (93%), and five of seven yearlings (71%) incubated a nest (including those that abandoned). There was no difference in nest initiation rates between years ($P = 0.11$). Nest initiation rate (including those that abandoned) for adult hens ($N = 20$) was 95% and did not differ ($P = 0.58$) from yearling hens (88%; $N = 16$). Nest initiation averaged 92% across age groups and years.

For nests in which we could determine clutch size ($N = 33$), average clutch size was 7.9 ± 0.5 eggs. There was no difference in clutch size between adults and yearlings ($P = 0.86$). We eliminated four nests from further analyses because we believed that they were abandoned because of disturbance from our field crews. In 2005, three of the nests were abandoned by the hen, and five were depredated. In 2006, one nest was abandoned by the hen, and eight nests were depredated.

The average distance from nests to the lek at which a hen was captured was $4.9 \text{ km} \pm 4.1$ ($\bar{x} \pm \text{SE}$), and it did not differ ($P = 0.67$) between successful and unsuccessful nests. The average distance from nests to the nearest lek was $2.7 \text{ km} \pm 2.4$. Unsuccessful nests did not differ from successful nests in relation to distance to the nearest lek ($P = 0.45$). Average distance to the nearest lek did not differ ($P = 0.45$) between years nor ($P = 0.77$) between adults or yearlings.

Nest selection

Of all nests, 85% were located under Wyoming big sagebrush ($N = 29/34$). Other than sagebrush, one nest was located beneath each four-wing saltbush *Atriplex canesens*, eastern redcedar *Juniperus virginiana* and wheat stubble *Triticum* spp., and two were beneath sweet clover. Vegetation at random sites was sparse, but slightly taller than at nest sites. Sage-grouse nest sites had greater ($P \leq 0.05$) percent canopy cover of total vegetation (total cover), grass cover, forb cover, sagebrush cover and litter (Table 1). Moreover, nest sites had greater visual obstruction at the nest (nest VOR) and surprisingly even greater visual obstruction 1 m away (1-m VOR). Although vegetation was taller at random sites, VOR for nest sites was greater ($P < 0.01$) than for random sites. Sagebrush density also was greater ($P < 0.01$) at nest sites than at random sites (see Table 1). Intermediate wheatgrass *Thinopyrum intermedium* was the only dominant grass with greater canopy cover at random sites; otherwise canopy cover of dominant grasses was greater at nest sites. Nonetheless, grass height and shrub height were marginally taller ($P > 0.07$) at random sites.

We included models with total cover, shrub density, shrub height, grass height, nest VOR and 1-m VOR in the evaluation of nest resource selection. Other variables were excluded because of correlations with these variables. Because total cover exhibited the smallest individual variable deviance, we constructed iterations of models around this variable. Of the 25 models we considered, five models were included in the set with $AIC_c < 2$ (Table 2). Two models, both including total cover and shrub height, with nest VOR (highest rank), and 1-m VOR (second-highest rank) best explained the nest resource selection by female sage-grouse. Nest sites were positively associated with greater percent total cover, greater 1-m VOR and nest VOR, and negatively related to shrub height. The third ranked model included only total cover and shrub height. Models that also included grass height, although ranked in

Table 1. Average of key vegetative (±SD) characteristics from greater-sage grouse nest sites and random sites included in resource selection models from North Dakota, USA, during 2005-2006. P-values as obtained using the multiple response permutation procedure (Mielke & Berry 2001).

	Nest		Random		
Vegetative characteristic	$\bar{x}$	±SD	$\bar{x}$	±SD	P-value
Total vegetative cover (%)	70.4	15.5	54.4	20.4	>0.01
Total grass cover (%)	27.4	13.6	19.3	14.6	0.01
Total forb cover (%)	15.4	11.8	11	6.6	0.05
Shrub cover (%)	9.8	4	7.1	4.6	>0.01
Litter (%)	12.9	8.3	7.9	5	0.01
Intermediate wheatgrass (%)	1.7	2.3	2.4	2.1	0.06
Green needlegrass (%)	2.5	3.3	1.3	1.8	0.06
Western wheatgrass (%)	4.2	3.7	2.1	2.6	<0.01
Kentucky bluegrass (%)	3.3	3.7	1.9	2.7	0.05
Nest VOR (inches)	2.6	1.2	2.1	1.6	0.02
1-m VOR	3.9	2.1	2.7	2.3	>0.01
2-m VOR	3	2.1	2.73	2.3	<0.01
3-m VOR	2.5	1.4	2.2	1.8	0.12
4-m VOR	2.4	1.5	2.1	1.8	0.3
5-m VOR	2.2	1.3	2.2	2.1	0.24
Site VOR	2.6	1.2	2.1	1.6	0.02
Sagebrush density (ha)	2576.1	1833.6	1399.4	1795.1	>0.01
Grass height (inches)	10.2	3.7	11.2	3.3	0.17
Shrub height (mm)	42.1	18.4	48.4	16.7	0.07

the 'supported' set, did not improve the deviance suggesting that grass height was not really important in describing the resource selection by nesting sage-grouse. The odds ratios indicated that nest VOR was the most important of the variables in the model. An increment of 2.54 cm for nest VOR increased the predicted probability of the site to be a nest by 16% ± 1% (95%CI). Increasing total vegetative cover by 10% increased the predicted probability of the site being selected for nesting by 0.60% ± 0.3% (CI 95%). Finally, the odds ratio for shrub height indicated a 9.1% ± 1.3% decrease in the predicted probability of a nest with each 1 cm increase in shrub height. Classification accuracy of the model was acceptable with an ROC value of 0.82. Odds ratios for the second ranked model were virtually identical to the previous model, except that greater weight was placed on the 1-m VOR.

Nest survival

We included 14 hens in nest survival analyses in 2005 (eight yearlings and six adults), and 15 hens were included in nest survival analyses in 2006 (three yearlings and 12 adults). Nest survival did not differ between years ($P < 0.05$). Estimated constant nest survival was 33% in 2005 ($N = 14$) and 30% in 2006 ($N = 15$).

The best model from the nest site selection (see above) was the lowest ranked model describing nest survival of the 41 models considered (Table 3). There was virtually no support for any of the single variable models. We included precipitation, constant survival, nest age and year in the table because they are often variables of interest despite their lack of support in our models. These were the same three top models when we included only vegetation characteristics (minus precipitation). Before including pre-

Table 2. Summary of model selection of logistic regression for greater sage-grouse nests ($N = 34$) from random sites ($N = 50$) in North Dakota, USA, during 2005-2006 using the Information Theoretic approach.

Model[1]	AIC	AIC_c	$AICw_i$	K[2]	Deviance
Total cover + shrub height + nest VOR	95.14	0	0.23	5	84.37
Total cover + shrub height + 1-m VOR	95.52	0.39	0.18	5	84.76
Total cover + shrub height	96.17	1.03	0.13	4	87.66
Total cover + shrub height + 1-m VOR + grass height	97.113	1.97	0.08	6	84.02
Total cover + shrub height + nest VOR + grass height	97.12	1.98	0.08	6	84.03
Global model	104.48	9.34	<0.01	10	81.47

[1]A total of 25 models were considered. Model results are presented in descending order of rankings and include models with AIC values <2.0.
[2]Number of parameters includes those in model plus year and the intercept.

Table 3. Summary of model selection for greater sage-grouse nest survival considering vegetation characteristics and time-dependent variables in southwestern North Dakota, USA, during 2005-2006.

Models[1]	AIC_c[2]	AIC_c	AIC_w[3] i	K[4]	Deviance
Grass height + shrub cover + nest VOR + precipitation	109.537	0	0.291 (0.376)	5	99.38
Grass height + shrub cover + total cover + nest VOR + precipitation	110.038	0.5	0.226	6	97.82
Grass height + shrub cover + nest VOR + site VOR + precipitation	111.129	1.59	0.13 (0.170)	6	105.45
Grass height + shrub cover + nest VOR	113.565	4.02	0.039	4	105.46
Precipitation	115.888	6.35	0.014	2	111.86
Constant survival	119.025	9.49	0.002	1	117.02
Nest age	120.219	10.68	0.001	2	116.19
Year	120.894	11.38	0.001	2	116.86
Best nest site selection model: total cover + shrub height + nest VOR	122.586	13.319	<0.001	4	114.751

[1]A total of 41 models were evaluated. We evaluated vegetation characteristics first, then included precipitation and temperature. The first three models were the highest ranked models with or without precipitation.

[2]Methods and interpretation of heading are described by Burnham & Anderson (2002).

[3]AIC_w in parentheses are those with the second model eliminated.

[4]Number of parameters in the model includes the intercept from constant survival estimate.

cipitation, AIC_w for these models were 0.15, 0.14 and 0.06, respectively. Although precipitation by itself provided little insight into nest survival of sage-grouse, when included with vegetation characteristics, the three top vegetation models showed strong support, with the fourth best model including just vegetation.

Evaluation of the coefficients of the second ranked model suggested that adding total cover to the model brought in some strong variable interactions causing the intercept to be below zero. Therefore, we eliminated this model and AIC_w assigned to models without this are in parentheses. Unequivocally, the model with the greatest support was the model including grass height, shrub cover, nest VOR and precipitation. The addition of site VOR to the highest ranked model contributed very little reducing the deviance in the model. Therefore, we were left with the highest ranked model to interpret.

Survival of sage-grouse nests was positively associated with grass height and shrub cover, and negatively associated with precipitation and nest VOR. The relation between nest VOR and survival seemed counter-intuitive, so we examined measurements of the nest shrub and found that successful nests were indeed in shorter shrubs than unsuccessful nests. None of the 95% CIs for odds ratios included 0. Grass height and shrub cover increased the probability of nests surviving by about 1.2% for each unit increase. An increase in nest VOR of 2.5 cm decreased the chances of the nest surviving by 2%, and 1 cm of precipitation decreased the chances of a nest surviving by about 7%. Daily precipitation had a consistent negative effect on nest survival (Fig. 1), which was amplified when shrub cover was less than about 9% or when grass height was less than about 16 cm (see Fig. 1C).

Discussion

Breeding chronology and nesting

Average clutch size in southwestern North Dakota was similar to the average clutch size found throughout the range of sage-grouse (Wallestad & Pyrah 1974, Sveum 1995). Despite predictions of age-specific differences in clutch size (Wallestad & Pyrah 1974, Petersen 1980), adults and yearlings had similar clutch sizes in our study.

We interpret the earlier nesting by adults to their being physiologically more mature and ready for reproduction than yearlings (e.g. Schroeder 1997). Improved habitat (nutritional) quality was postulated to be responsible for increased production in sage-grouse in Oregon (Barnett & Crawford 1994), and Gregg et al. (2006) showed that hens with greater plasma protein were more likely to renest. The low renesting rate in our study suggests that some aspect of the habitat was lacking.

Sage-grouse do not always nest near a lek and may nest independent of lek locations (Bradbury et al. 1989, Wakkinen et al. 1992a). In Alberta Canada, less than ½ of the nests (41%) were within 3.2 km of the lek (Aldridge & Brigham 2001). However elsewhere, most nests occur within 3.2 km of leks (Braun et al. 1977). The population of sage-grouse which we studied was non-migratory, 68% of nests were within 3.2 km of a lek and 86% of nests were within 5 km of a lek. It is likely that suitable nesting habitat

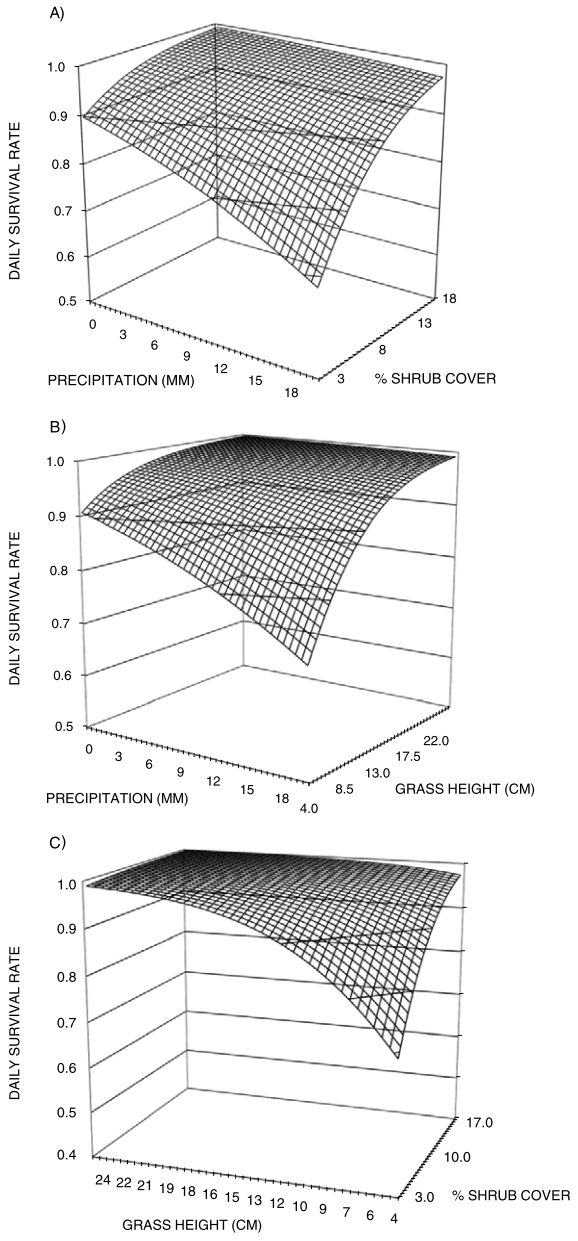


Figure 1. Daily survival as a function of precipitation and percent shrub cover with nest VOR and grass height constant at mean (A), precipitation and grass height with nest VOR and percent shrub cover held constant at the mean (B), and grass height and shrub cover with precipitation and nest VOR held constant and the mean (C).

for sage-grouse in the Dakotas, at the eastern fringe of sage-grouse range, occurs near leks. Aldridge & Brigham (2001) came to a similar conclusion for a population at the northern fringe of the sage-grouse range. While in more contiguous sagebrush of Wyoming, there was less propensity for sage-grouse to nest near the lek (Holloran & Anderson 2005).

Nest selection

Most studies describe the importance of sagebrush canopy cover and herbaceous canopy cover (Wakkinen 1990, Connelly et al. 1991, Sveum et al. 1998, Hagen et al. 2007) for sage-grouse nesting habitat. However, in southwestern North Dakota, nest resource selection may take on different characteristics than other portions of the sage-grouse range. Sage-grouse usually nest in taller sagebrush (Connelly et al. 2000) and often select the tallest sagebrush (Wakkinen 1990, Apa 1998). However, in our study, sage-grouse selected sites with greater vegetative cover and greater visual obstruction at and near the nest, but with shorter shrub height than was available in the area. Tall grass can also be an important contributor to concealment of sage-grouse nests (Connelly et al. 1991, Gregg et al. 1994), and although grass height was included in the models with marginal support, it too was shorter than at our random sites. In this area, where the sagebrush steppe transitions to mixed grass prairie, sagebrush occurs in higher densities on range sites in low seral condition and soils with low productivity. Vegetative productivity on these sites can be reduced by overgrazing by livestock (Natural Resources Conservation Service, Electronic Field Office Technical Guide, available at: http://efotg.nrcs.usda.gov/efotg_locator.aspx?map=ND; last accessed on 25 November 2008). Thus, it is not surprising that taller grass and taller shrubs (sagebrush) occurred on sites where sagebrush was less prominent. Despite the nuances of site characteristics, sage-grouse appeared to select for greater concealment at and near the nest, and other than vegetative cover nest area variables were not important to nest selection by sage-grouse in our area.

Nest survival

Across the range, sage-grouse nest survival averages just under 50% in relatively unaltered habitats and below 40% in altered habitats (Connelly et al. 2004). Nest success in stable populations generally tends to be higher (Aldridge & Brigham 2001). The population of sage-grouse which we studied would likely be considered unstable (declining) from 1951 to present (unpubl. spring sage-grouse census data; North Dakota Game and Fish Department, Bismarck, North Dakota). Most of the area has been altered by historical grazing, and oil and gas development. Nest survival in our study was typical of other altered habitats and most nests were lost to predation. While marking nests and repeat visitations to nests could attract predators, we visited nest sites only

once to estimate the stage of incubation and otherwise stayed >20 m away, and we do not believe that inconspicuous flagging on sagebrush 20 m from nests increased nest predation. Nest predation can be higher in fragmented landscapes (Herkert 1994, Sievert & Lloyd 1985). In the Powder River Basin of Wyoming, extensive large-scale modifications of sagebrush habitat, and range modification for livestock from oil and gas development were associated with significant reductions in sage-grouse populations (Walker et al. 2007).

Of the vegetative characteristics identified in the resource selection models for nests, only nest VOR was included in models of nest survival; and it had a negative relation to daily survival rates. The height of the shrubs under which nests were located was also lower at nests that survived than those that failed. We attribute these counter-intuitive relations to selection by sage-grouse for area of higher shrub/sagebrush which had a positive influence on survival of nests. Thus, our data suggested that shrub (sagebrush) cover may be more important than taller shrubs in nest survival. Areas with high shrub cover also had relative low stature sagebrush. The low stature of sagebrush in these stands likely resulted from the dense clay-pan soils or past grazing practices. Connelly et al. 2000 reviewed several studies that showed sage-grouse selecting stands with greater sagebrush cover, but also the tallest sagebrush in the stand. Tall grass improved daily survival rates and seemingly compensated to some degree for the shorter concealment by shrubs. When shrub cover was less than about 9-10% or grass height was less than about 16-18 cm nest survival declined rapidly. Although shrub cover was lower than found in most other studies, the grass height at nest sites in our study was reflective of other studies.

Predators with a keen sense of smell use olfactory cues to locate nests (Storaas 1988), and birds that are wet have been hypothesized to have stronger odour because water on the skin activates bacteria (Syrotuck 2000). Daily precipitation events decreased daily survival rates which declined in a near linear manner with increasing amounts of precipitation. Precipitation during incubation increased predation of wild turkey *Meleagris gallopavo* nests (Roberts et al. 1995, Roberts & Porter 1998, Lehman et al. 2008). However, the relation between precipitation and nest survival may be complicated by high nest attendance by the female and decreased predator activity during precipitation followed by a lag effect on subsequent days when females are away from the nest (Moynahan et al. 2007). However, the lag of precipitation was not important in our study.

Management implications

If the Bureau of Land Management (BLM) could increase its management buffer from the current 3.2 km (Resource Management Plan, Bureau of Land Management, Dickenson, North Dakota) to 5 km, this larger area would encompass 86% of nests. Currently, there are no management regulations that pertain to sage-grouse on state-owned land in North Dakota. We believe that a strategy similar to the BLM would be beneficial to sage-grouse. Our models suggest that patches of shrubs/sagebrush with >9% canopy cover and grass taller than 16 cm improved the chances of a sage-grouse surviving to hatch. Sagebrush patches selected by nesting females were grazed and showed evidence of being in low seral condition due to past grazing or soil characteristics. There is strong evidence in the literature that if areas of sagebrush cover (>9%) occurred with taller shrubs, sage-grouse would use them and it should improve nest survival. Tall grass is also important to sage-grouse nest survival and grazing management that provides grass heights of >16 cm should benefit nest survival. Our results emphasize the importance of considering local conditions in the management of sage-grouse.

Acknowledgements - funding for our study was provided by Federal Aid in Wildlife Restoration Act (W-67-R) through North Dakota Game and Fish Department, Bureau of Land Management (ESA000013), U.S. Forest Service, Rocky Mountain Research Station (05-JV-11221609-127), U.S. Forest Service Dakota Prairie National Grasslands (05-CS-11011800-022) and support from South Dakota State University. Field assistance was provided by A. Geigle, D. Gardner, C. Berdan and T. Zachmeier. A number of volunteers assisted during capture and radio-collaring of hens and chicks. T. Apa assisted with training on trapping techniques. We also acknowledge and appreciate the landowners who granted us permission to conduct this study on their lands. R. King provided statistical advice and support, and J. Connelly and C. Hagen provided comments to earlier drafts of this manuscript.

References

Aldridge, C.L. & Brigham, R.M. 2001: Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. - Condor 103: 537-543.

Apa, A.D. 1998: Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA, 199 pp.

Barnett, J.F. & Crawford, J.A. 1994: Pre-laying nutrition of sage grouse. - Journal of Range Management 47: 114-118.

Benkobi, L., Uresk, D.W., Schenbeck, G. & King, R.M. 2000: Protocol for monitoring standing crop in grasslands using visual obstruction. - Journal of Range Management 53: 627-633.

Booth, D.T., Cox, S.E., Meilke, T.W. & Fitzgerald, C. 2006: The accuracy of ground-cover measurements. - Rangeland Ecology and Management 59: 179-188.

Bradbury, J.W., Gibson, R.M. & McCarthy, C.E. 1989: Dispersion of displaying Sage Grouse males: II, the role of female dispersion. - Behavioral Ecology of Sociobiology 24: 15-24.

Braun, C.E., Britt, T.E. & Wallestad, R.O. 1977: Guidelines for maintenance of sage grouse habitats. - Wildlife Society Bulletin 5: 99-106.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 488 pp.

Connelly, J.W., Knick, S.T., Schroeder, M.A. & Stiver, S.J. 2004: Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats. - Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA, 610 pp.

Connelly, J.W., Schroeder, M.A., Sands, A.R. & Braun, C.E. 2000: Guidelines to manage sage grouse populations and their habitats. - Wildlife Society Bulletin 28: 967-985.

Connelly, J.W., Wakkinen, W.L., Apa, A.D. & Reese, K.P. 1991: Sage grouse use of nest sites in southeastern Idaho. - Journal of Wildlife Management 55: 521-524.

Cottam, G. & Curtis, J.T. 1956: The use of distance measures in phytosociological sampling. - Ecology 37: 451-460.

Crunden, C.W. 1963: Age and sex of sage grouse from wings. - Journal of Wildlife Management 27: 846-849.

Daubenmire, R.F. 1959: A canopy-coverage method of vegetation analysis. - Northwest Science 33: 224-227.

Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002: Advanced techniques for modeling avian nest survival. - Ecology 83: 3476-3488.

Floyd, D.A. & Anderson, J.E. 1987: A comparison of three methods for estimating plant cover. - Journal of Ecology 75: 221-228.

Gregg, M.A., Crawford, J.A., Drut, M.S. & Delong, A.K. 1994: Vegetational cover and predation of sage grouse nests in Oregon. - Journal of Wildlife Management 58: 162-166.

Gregg, M.A., Dunbar, M.R., Crawford, J.A. & Pope, M.D. 2006: Total plasma protein and renesting by greater sage-grouse. - Journal of Wildlife Management 70: 472-478.

Guthery, F.S., Brennan, L.A., Peterson, M.J. & Lusk, J.J. 2005: Information theory in wildlife science: critique and viewpoint. - Journal of Wildlife Management 69: 457-465.

Hagen, C.A., Connelly, J.W. & Schroeder, M.A. 2007: A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. - Wildlife Biology 13(1): 42-50.

Hays, H. & LeCroy, M. 1971: Field criteria for determining incubation stage in eggs of the common tern. - Wilson Bulletin 83: 425-429.

Herkert, J.R. 1994: The effects of habitat fragmentation on Midwestern grassland bird communities. - Ecological Applications 4: 461-471.

Holloran, M.J. & Anderson, S.H. 2005: Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. - Condor 107: 742-752.

Hosmer, D.W. & Lemeshow, S. 2000: Applied Logistic Regression. 2nd edition. - John Wiley & Sons Incorporated Publication, New York, USA, 373 pp.

Johnson, J.R. & Larson, G.E. 1999: Grassland plants of South Dakota and the northern Great Plains. - South Dakota Agricultural Experiment Station B566 (rev.), South Dakota State University, Brookings, USA, 288 pp.

Klebenow, D.A. 1969: Sage grouse nesting and brood habitat in Idaho. - Journal of Wildlife Management 33: 649-662.

Lehman, C.P., Rumble, M.A., Flake, L.D. & Thompson, D.J. 2008: Merriam's turkey nest survival and factors affecting nest predation by mammals. - Journal of Wildlife Management 72: 1765-1774.

McCarthy, J.J. & Kobriger, J.D. 2005: Management plan and conservation strategies for greater sage-grouse in North Dakota. - North Dakota Game and Fish Department, Bismarck, North Dakota, USA, 7 pp.

Mielke, P.W. Jr. & Berry, K.J. 2001: Permutation Methods: a distance function approach. - Springer-Verlag, New York, New York, USA, 352 pp.

Moynahan, B.J., Lindberg, M.S., Rotella, J.J. & Thomas, J.W. 2007: Factors affecting nest survival of greater sage-grouse in northcentral Montana. - Journal of Wildlife Management 71: 1773-1783.

North Dakota Agricultural Weather Network 2006: Climatology Information, Bowman, North Dakota, USA. Available at: http://ndawn.ndsu.nodak.edu. (Last accessed on 5 September 2006).

Oyler-McCance, S.J., Taylor, S.E. & Quinn, T.W. 2005: A multilocus population genetic survey of the greater sage-grouse across their range. - Molecular Ecology 14: 1293-1310.

Patterson, R.L. 1952: The sage grouse of Wyoming. - Sage Books, Inc., Denver, Colorado, USA, 341 pp.

Petersen, B.E. 1980: Breeding and nesting ecology of female Sage Grouse in North Park, Colorado. - M.Sc. thesis, Colorado State University, Fort Collins, Colorado, USA, 86 pp.

Pollard, J.H. 1971: On distance estimators of density in randomly distributed forests. - Biometrics 27: 991-1002.

Robel, R.J., Briggs, J.N., Dayton, A.D. & Hulbert, L.C. 1970: Relationships between visual obstruction measurements and weight of grassland vegetation. - Journal of Range Management 23: 295-297.

Roberts, S.D., Coffey, J.M. & Porter, W.F. 1995: Survival and reproduction of female wild turkeys in New York. - Journal of Wildlife Management 59: 437-447.

Roberts, S.D. & Porter, W.F. 1998: Relation between weather and survival of wild turkey nests. - Journal of Wildlife Management 62: 1492-1498.

SAS Institute 2005: SAS: JMP Start Statistics. - SAS Publishing Incorporated, New York, USA. Available at: http://www.jmp.com

Schroeder, M.A. 1997: Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. - Condor 99: 933-941.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Diebert, P.A., Gardner, S.C., Hilliard, M.A., Kobriger, G.D. & McCarthy, C.W. 2004: Distribution of Sage Grouse in North America. - Condor 106: 363-376.

Sievert, P.R. & Lloyd, K.B. 1985: Survival of Snowshoe Hares at a Geographical Boundary. - Journal of Wildlife Management 49: 854-866.

Smith, J.T., Flake, L.D., Higgins, K.F., Kobriger, G.D. & Homer, C.G. 2005: Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. - Western North American Naturalist 65: 310-320.

SPSS 2002: SPSS for Windows 11.5. - SPSS, Inc., Chicago, Illinois. Available at: http://www.spss.com

Stephens, P.A., Buskirk, S.W., Hayward, G.D. & del Rio, C.M. 2005: Information theory and hypothesis testing: a call for pluralism. - Journal of Applied Ecology 42: 4-12.

Storaas, T. 1988: A comparison of losses in artificial and naturally occurring capercailiie nests. - Journal of Wildlife Management 52: 123-126.

Sveum, C.M. 1995: Habitat selection by Sage Grouse hens during the breeding season in south-central eastern Washington. - M.Sc. thesis, Oregon State University, Corvallis, Oregon, USA, 86 pp.

Sveum, C.M., Edge, W.D. & Crawford, J.A. 1998: Nesting habitat selection by sage grouse in southcentral Washington. - Journal of Range Management 51: 265-269.

Syrotuck, W.G. 2000: Scent and the scenting dog. - Barkleigh Productions, Inc., Mechanicsburg, Pennsylvania, USA, 111 pp.

Wakkinen, W.L. 1990: Nest site characteristics and spring-summer movements of migratory Sage Grouse in southeastern Idaho. - M.Sc. thesis, University of Idaho, Moscow, Idaho, USA, 57 pp.

Wakkinen, W.L., Reese, K.P. & Connelly, J.W. 1992a: Sage grouse nest location in relation to leks. - Journal of Wildlife Management 56: 381-383.

Wakkinen, W.L., Reese, K.P., Connelly, J.W. & Fischer, R.A. 1992b: An improved spotlighting technique for capturing Sage Grouse. - Wildlife Society Bulletin 20: 425-426.

Walker, B.L., Naugle, D.E. & Doherty, K.E. 2007: Greater sage-grouse population response to energy development and habitat loss. - Journal of Wildlife Management 71: 2644-2654.

Wallestad, R.O. & Pyrah, D.B. 1974: Movement and nesting of sage grouse hens in central Montana. - Journal of Wildlife Management 38: 630-633.

Welch, B.L. 2005: Big sagebrush: as sea fragmented into lakes, ponds, and puddles. - U.S. Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-144, Fort Collins, Colorado, USA, 210 pp.

White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. - Bird Study 46: 120-138.

Check for updates

Received: 22 July 2021 | Revised: 26 February 2022 | Accepted: 12 March 2022

DOI: 10.1002/wat2.1592

PERSPECTIVE

WIREs WATER WILEY

Beaver: The North American freshwater climate action plan

Chris E. Jordan[1] | **Emily Fairfax**[2]

[1]NOAA NMFS Northwest Fisheries Science Center, Newport, Oregon, USA

[2]California State University Channel Islands, Camarillo, California, USA

Correspondence
Emily Fairfax, California State University Channel Islands, 1 University Drive, Camarillo, CA 93012, USA.
Email: emily.fairfax@csuci.edu

Edited by: Jan Seibert, Editor-in-Chief

Abstract

Rivers and streams, when fully connected to their floodplains, are naturally resilient systems that are increasingly part of the conversation on nature-based climate solutions. Reconnecting waterways to their floodplains improves water quality and quantity, supports biodiversity and sensitive species conservation, increases flood, drought and fire resiliency, and bolsters carbon sequestration. But, while the importance of river restoration is clear, beaver-based restoration—for example, strategic coexistence, relocation, and mimicry—remains an underutilized strategy despite ample data demonstrating its efficacy. Climate-driven disturbances are actively pushing streams into increasingly degraded states, and the window of opportunity for restoration will not stay open forever. Therefore, now is the perfect time to apply the science of beaver-based low-tech process-based stream restoration to support building climate resilience across the landscape. Not every stream will be a good candidate for beaver-based restoration, but we have the tools to know which ones are. Let us use them.

This article is categorized under:

Science of Water > Hydrological Processes

Water and Life > Nature of Freshwater Ecosystems

Water and Life > Conservation, Management, and Awareness

KEYWORDS

beaver, climate change, floodplain connectivity, process-based restoration, water security, wildfire

1 | INTRODUCTION: BEAVERS, THE CLIMATE ACTION PLAN

Low-tech process-based stream restoration (LTPBR)—a suite of simple, low-cost practices focused on floodplain reconnection—is rapidly gaining traction in the face of looming climate and biodiversity crises (Ciotti et al., 2021;

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the Department of Commerce.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *WIREs Water* published by Wiley Periodicals LLC.

Davee et al., 2019; Davis et al., 2021; Johnson et al., 2019; Keeble-Toll, 2018; Munir & Westbrook, 2020; Pearce et al., 2021a, 2021b; Silverman et al., 2019; Wade et al., 2020; Weber et al., 2017; Wheaton et al., 2019). Though the implementation of these methods has a strong theoretical and technical foundation, skepticism lingers—particularly about the efficacy of hand-built, beaver-inspired structures, and beaver coexistence. In particular, recent publications have called into question the practicality of achieving watershed-scale changes through beaver landscape modifications or anthropogenic beaver mimicry (Nash et al., 2018; Nash et al., 2021; Pilliod et al., 2017). This is despite countless of years of Indigenous knowledge on sustainable riparian and beaver management (Albert & Trimble, 2000; Blackfeet Nation, 2018; Blackfeet Nation & Levitus, 2019; Feit, 1986; Gadgil et al., 1993; Keeble-Toll, 2018; Kimmerer, 2000; Kimmerer & Lake, 2001; Sherriff, 2021) and over a century of published data, experiments and analyses (Ives, 1942; Morgan, 1868; Neff, 1957; Ruedemann & Schoonmaker, 1938; Seton, 1929) documenting enhanced hyporheic engagement (Briggs et al., 2013; Janzen & Westbrook, 2011; X. Wang et al., 2018), improved water quality (Cornell et al., 2011; Lazar et al., 2015; Puttock et al., 2017, 2018; Shepherd & Nairn, 2020, 2021), naturalized flow timing (Burchsted et al., 2010), failure of traditional engineering approaches to restoration (D. M. Thompson & Stull, 2002), and wildfire resilience (Fairfax & Whittle, 2020; Foster et al., 2020; Weirich, 2021; Whipple, 2019). Fully floodplain-connected, beaver-occupied riverscapes (Brazier et al., 2021; Larsen et al., 2021) are natural process domains we can no longer afford to ignore.

It may seem trite to say that beavers are a key part of a national climate action plan, but the reality is that they are a force of 15–40 million (Naiman et al., 1988) highly skilled environmental engineers. We cannot afford to work against them any longer; we need to work with them. In most cases, the first step will be starting the physical restoration process before beavers move into a system—setting the stage for functioning floodplain processes (flow, space, structure; Beechie et al., 2010, Cluer & Thorne, 2014, Wheaton et al., 2019). Human intervention may be necessary to restore severely impacted floodplain processes to the point at which beavers and beaver mimicry can be applied (e.g., deeply incised channels, ongoing disruptive land-use practices). In other situations, our first step may be policy changes: for example, if floodplains are intact, but beaver management actions (e.g., the lethal removal of beavers that impact the built environment) prevent population persistence sufficient to further recover these landscapes. Regardless of our role in the conversation, beaver inspired or implemented process-based restoration should be a primary strategy to achieving healthy riverscapes (Macfarlane et al., 2015; Pollock et al., 2015). A stream where beavers thrive is a resilient, productive stream (Pollock et al., 2014). Flourishing beaver populations can be our partner in combating climate change and a bellwether of our progress.

2 | RIVERSCAPE RESTORATION IS THE LOW-HANGING FRUIT

A changing climate amplifies the impacts of impaired riverscapes: more frequent extreme precipitation events in over-capacity channels lead to more flooding (Stott, 2016); increasing air temperature and drier conditions stress valley-bottom vegetation already isolated from hyporheic aquifers, driving wildfires into "megafires" (Finco et al., 2012; Goss et al., 2020; Mori & Johnson, 2013; Swain, 2021; J. Williams, 2013; A. P. Williams et al., 2019); and snow-driven flow regimes shifting to rain-driven bring lower, warmer base-flows and further degraded biotic conditions (Beechie et al., 2013). However, we are not developing riverscape-scale nature-based climate action strategies (Skidmore & Wheaton, 2022). Restoring floodplain connectivity and function is both a climate change mitigation and adaptation strategy because it reverses degradation and recovers natural resilience (Johnson et al., 2019; Pollock et al., 2015; Silverman et al., 2019; Wheaton et al., 2019). Natural riverscape resilience is only achieved through a restoration of floodplain processes (Cluer & Thorne, 2014), not the engineering or imposition of form (ELI, 2016).

The US EPA's latest assessment rates the flowing waters of the United States (CONUS only) as being in less than good condition (e.g., 25%–50% in poor condition; USEPA, 2013). Human activity has drastically reduced floodplain connectivity across the continent, converting valley spanning wetlands to narrow riparian corridors. For example, in the Sacramento Valley of California, riparian forests on well-connected floodplains have been reduced from 24% to less than 0.5% of the land area (Sands & Howe, 1977). Our activities over the last two centuries have reduced active floodplain area by an order of magnitude and degraded half the flowing waters in the United States. Human degradation of riverscapes, left unchecked, creates positive feedback cycles of further degradation under a changing climate (Figure 1). However, beaver-based restoration creates profound opportunities for initiating positive feedback cycles and increasing riverscape resilience.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

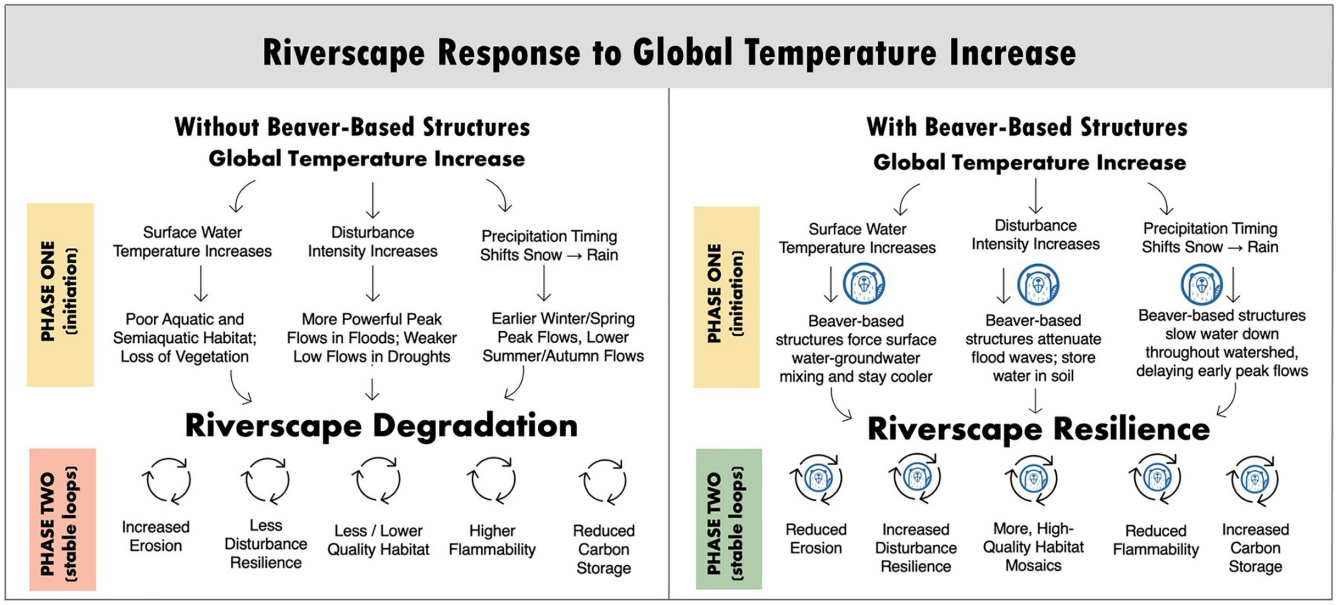


FIGURE 1 Comparison of riverscape feedback cycles with increased global temperature. Phase 1 indicates processes that are initiated by warming global temperatures and lead to either degradation or resilience. Phase 2 indicates processes that occur once riverscapes have already reached a degraded or resilient state. Left: Cycle of increasing riverscape degradation occurring without beaver or beaver mimicry. Right: Cycle of maintained riverscape resilience that can be achieved by partnering with beaver and utilizing beaver-based designs

3 | THE INTERCONNECTED BIOLOGY, HYDROLOGY, AND GEOMORPHOLOGY OF FLOODPLAIN RESILIENCE

Watersheds are typically described by the physical aspects (e.g., flow direction and rate, area, gradient, precipitation, geology) that are thought to drive all characterizing properties (Kasprak et al., 2016). However, watersheds are much more than the sum of their physical properties (Fausch et al., 2002). Watersheds, as riverscapes, are energetically rich, dynamic, bio-geomorphic systems. In temperate mesic climate zones, riverscapes have up to six orders of magnitude more potential energy (chemical) stored in organic material (both live and in the decomposer cycle) than the potential energy (physical) of the in-channel flow (Phillips, 2016). Connected floodplains are more productive than disconnected floodplains in part because of their ability to retain and extract the chemical potential energy of the watershed's biotic (organic) components (Puttock et al., 2018; Wegener et al., 2017). Functioning floodplains are connected because planform and longitudinal structures increase resistance to surface water movement, force water up onto floodplain surfaces, and form a diversity of flow paths across the entire valley-bottom (Pollock et al., 2014; Wheaton et al., 2019). This in-channel and across-floodplain hydraulic roughness dissipates flow energy, keeping the transport-deposition balance more to the deposition side, but more importantly, increasing the residence time of surface and hyporheic aquifer water, thereby shortening the length scales of nutrient spirals and increasing ecosystem productivity (Briggs et al., 2013; Helton et al., 2014). Connected-floodplain systems are hydrologically inefficient, a necessary, but often overlooked characteristic.

Many impaired streams, rivers, and associated floodplains are in a state that is physically stable, but simplified and degraded (Cluer & Thorne, 2014). Connected-floodplain systems are dynamic (Naiman et al., 2010). They are in a quasi-equilibrium state across many forcing processes, and thus are inherently more resilient to disturbance than impaired streams (Silverman et al., 2019; Wohl, 2021a; Wohl et al., 2017, 2021). But, maintaining the quasi-equilibrium condition of a connected floodplain requires continual energetic input. This situation is similar to many well-studied coastal marine bio-geomorphic systems—including fringing coral reefs, mangrove swamps, and salt marshes—systems driven by the physics of waves, tidal currents and flowing freshwater, but forced by their biological components (Alongi, 2008; Dame & Patten, 1981; Johnson et al., 2019; Pethick, 1992).

In bio-geomorphic systems, plants and animals form structures that modify the physical environment, resulting in a more productive ecosystem (biomass generated per unit area per unit time) than the same location would be without the structure (Viles, 1988; C. Wang et al., 2020). However, once a bio-geomorphic system has been degraded, it does not

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

take much to keep it that way (Castro & Thorne, 2019). Restoring high-energy, simplified systems requires re-establishing the biological control of the geomorphic setting (Johnson et al., 2019). In floodplains many of the most important sources of external energy are biological inputs, including organic material deposition, vegetation growth, and beaver dam building. Therefore, embracing ecosystem engineers like beaver is the fast track to low-cost, high-impact sustainable riverscape connectivity (Brazier et al., 2021; Dittbrenner et al., 2018; Johnson et al., 2019; Pollock et al., 2007, 2014).

4 | BENEFITS OF FLOODPLAIN-CONNECTED RIVERS IN A WARMING WORLD

Restoring and reconnecting floodplains clearly provides a myriad of benefits. A floodplain-connected valley is inherently more diverse and productive, not only for aquatic species, but across the entire floodplain (Bellmore & Baxter, 2014). On the seasonally wet floodplain surface, vegetation productivity and plant and animal species richness and diversity are higher than on a disconnected, permanently dry terrace (Stella et al., 2011). In the channels of a connected floodplain reach, primary productivity is higher, macroinvertebrate communities are richer and more productive (Nummi et al., 2021; Robinson et al., 2020), and amphibian and fish productivity is higher (Anderson et al., 2015; Bouwes et al., 2016; Dauwalter & Walrath, 2018; Romansic et al., 2021; Wathen et al., 2019) than in simple channels of a disconnected reach. But, while these internal benefits are independently valuable, they are only a small fraction of the potential benefits that restored riverscapes can provide in the face of climate change. When we reconnect streams and rivers to their floodplains, we perform both climate mitigation work (slowing/stopping the trajectory of global warming) and climate adaptation work (building resilience and resistance to climate-driven disturbances that are already occurring; see Table 1).

4.1 | Slow water—flood, drought, and fire resilience

A diversity of water residence times in a river system enhances the riverscape's ability to attenuate peak flows during wet periods and release stored water as base flow during dry periods, simultaneously mitigating against both drought and flood (Fairfax & Small, 2018; G. A. Hood & Bayley, 2008; G. A. Hood & Larson, 2015; Puttock et al., 2021; Westbrook et al., 2006, 2020). This also helps keep water in the soil during periods of prolonged drought, where it is accessible to riparian vegetation (Amlin & Rood, 2003; Dittbrenner et al., 2018; Fairfax & Small, 2018; Puttock et al., 2021; Silverman et al., 2019; Vivian et al., 2014). However, floodplain-connected riverscapes function as speed bumps to fire spread because the soil, vegetation, and stream channels are wet throughout, and thus do not readily burn (Fairfax & Whittle, 2020; Weirich, 2021; Whipple, 2019; Wohl et al., 2022). Therefore, long stretches of restored floodplains could function as a network of firebreaks, slowing the spread of wildfires and giving humans time to contain runaway wildfires before they reach a dangerous, out-of-control state (Fairfax & Whittle, 2020).

4.2 | Clean, cool water—bolstered aquatic biodiversity

Floodplain-connected riverscapes have more large wood (loose wood, logjams) both on the ground and in the channel. Woody deposits in general increase the physical forcing of stream and floodplain structure and increase water residence time and primary productivity at the floodplain surface (Appling et al., 2014; Briggs et al., 2013; Collins et al., 2012; Helton et al., 2014; Magilligan et al., 2008; Osei et al., 2015; Poole et al., 2008). But, beaver-managed vegetation and stream hydraulic modification (dams, lodges, canals) function similarly, because they directly increase hydraulic diversity and vegetation productivity (Silverman et al., 2019). Thus, hydraulic inefficiency, no matter the source, results in longer water residence time and increased nutrient cycling, which in turn enhances biological productivity across all trophic levels.

Wetlands, inundated floodplains, deep pools, and other areas of slow water within riverscapes help sink out and process common aquatic pollutants such as nitrates, phosphates, metals, and excess sediments (Klotz, 1998, 2010; Kroes & Bason, 2015; Maret et al., 1987; Muskopf, 2007; Puttock et al., 2017, 2018; Shepherd & Nairn, 2020, 2021; Short et al., 2015). Some pollutants bind onto fine sediments which remain suspended in the water column until reaching

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Briefly summarizes how connected- and disconnected-floodplain riverscapes generally respond to several key aspects of climate change (with abbreviated selected references)

	Disconnected floodplains	Connected floodplains	Abbreviated selected references
Water temperature (adaptation)	Homogenous, warmer	Heterogenous, cooler	Majerova et al., 2015, Weber et al., 2017, Dauwalter & Walrath, 2018; Lowry, 1993, Romansic et al., 2021
Carbon (mitigation)	Lower sequestration potential	Higher sequestration potential	Wohl, 2013, Laurel & Wohl, 2019
Floods (adaptation)	Low capacity to accommodate flood waves, higher erosion rates on channel banks from more powerful peak flows	High capacity to accommodate flood waves, lower erosion on channel banks from dissipated peak flows	Westbrook et al., 2006, Westbrook et al., 2020, Puttock et al., 2021
Droughts (adaptation)	Low capacity to maintain primary productivity during extended dry periods	High capacity to maintain primary productivity during extended dry periods	G. A. Hood & Bayley, 2008, Fairfax & Small, 2018, Dittbrenner et al., 2018
Fires (adaptation)	Higher fuel flammability. Loss of riparian vegetation leads to intense post-fire debris entering river from surrounding area	Lower fuel flammability. Intact riparian vegetation slows debris entering river from surrounding area. In-stream structures trap sediment and aggrade within channel, reversing prior channel incision	Fairfax & Whittle, 2020, Wohl et al., 2022, Weirich, 2021, Whipple, 2019

low velocity reaches. Once these fine sediments are either deposited on the floodplain or settled at the bottom of ponds and wetlands, naturally occurring biogeochemical processes transform potent nutrients (e.g., nitrate) into inert compounds (e.g., gaseous nitrogen) or facilitate re-uptake in aquatic vegetation (Yousaf et al., 2021). But, systematic approaches to nature-based riverscape-scale pollution mitigation are lacking, and re-establishing the natural biogeochemical balance of recently restored stream-wetland systems takes time (Weigelhofer et al., 2018). Therefore, structures within streams and rivers, such as natural or artificial beaver dams or better floodplain connection can serve as a network-wide natural mitigation tactic. For example, implementation of LTPBR, especially Beaver Dam Analogs (BDAs), is gaining popularity as a post-fire, land-management strategy to attenuate post-fire debris flows and reduce the suspended ash and soot in the water column (Short et al., 2015).

Many aquatic species have strict water temperature requirements that are regularly exceeded as the climate warms. Structures within rivers, whether human built bio-geomorphic mimics (e.g., Post-Assisted Log Structure [PALS, BDAs]) or naturally occurring (beaver dams, woody debris), generate vertical hydraulic pressure gradients, forcing some of the streamflow down through the river bottom and into the hyporheic zone (Munir & Westbrook, 2020; Scamardo & Wohl, 2020; Wade et al., 2020). There, warm surface water and typically cooler subsurface water can mix before returning to the river downstream (Weber et al., 2017). The residence time of water on these flow paths varies; as a result, so does the temperature of the water as it returns to the river. However, the resulting highly heterogeneous thermal profile of the riverscape supports a variety of aquatic life with different temperature needs (Dauwalter & Walrath, 2018; Lowry, 1993; Majerova et al., 2015, 2020; Romansic et al., 2021). Therefore, in-stream structure, or connected floodplains are a critical component of naturally functioning riverscapes.

4.3 | Complex water pathways—carbon storage and habitat mosaics

Hydrologically complex riverscapes provide a diversity of intermingled habitats that support a vast array of plant and animal species. Naturally occurring beaver dam complexes are uniquely rich and varied components of riverscapes that contain highly heterogeneous water velocities, temperatures, depths, vegetation communities, and geomorphic structures within relatively small areas of the riverscape (Larsen et al., 2021; Rosell et al., 2005; Stringer & Gaywood, 2016). This heterogeneity results in particularly diverse and resilient habitats and is a large part of why beavers are keystone

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

species (Hammerson, 1994; Naiman et al., 1986; Naiman et al., 1988; Pollock et al., 1995). But, this key bio-fluvial component of riverscapes is rare because a long history of anthropogenic impacts has simplified and disconnected streams from their floodplains (Fouty, 2018). Therefore, floodplain reconnection is often invoked to improve the quantity and quality of physical and biological habitat characteristics needed by fish, amphibians, waterfowl, and other aquatic and semi-aquatic species (Anderson et al., 2015; Baldwin, 2015; Dauwalter & Walrath, 2018; W. G. Hood, 2012; Kauffman et al., 1997; McKinstry et al., 2001; Pollock et al., 2004; Romansic et al., 2021; Snodgrass & Meffe, 1998; Wathen et al., 2019; Wohl, 2021b; Wohl et al., 2021).

The complexity of floodplain-connected rivers increases carbon storage via several mechanisms, including bolstered sequestration in riparian forests and enhanced deposition of organic-rich sediments and deposits of fibrous carbon in periodically and regularly flooded environments (Laurel & Wohl, 2019). But, beaver dam-building activity can increase carbon storage even further via additional streamflow velocity reduction, regular tree coppicing, the expansion of periodically flooded land area, and the frequent inundation of between 10% and 30% of the valley bottom at baseflow. Even relic/inactive beaver-dammed areas store significantly more carbon than those without a recent history of beaver. Recent research indicates that grasslands (which often replace riparian forest in degraded river systems) store on average 40–100 metric tons of carbon per hectare while active and inactive/relic beaver complexes store 1150–1400 and 300–400 metric tons of carbon per hectare, respectively (Wohl, 2013). However, the complete carbon budget of beaver modified floodplains is a spatially and temporally complex balance. Carbon locked up in dead standing vegetation and in organic material deposited in the stream and pond bed is offset by CO_2 and CH_4 emissions from the decomposer cycle. Though not well documented, the net balance is estimated to range from source to sink, depending on pond age, temperature, and soil and vegetation type (Nummi et al., 2018). Thus, riverscape restoration, particularly floodplain restoration with beaver, can support a significant increase in landscape carbon storage, and provide climate mitigation as well as adaptation benefits, though questions remain regarding the factors mediating net carbon storage and thus our ability to design and generalize across all settings.

4.4 | Floodplain dynamics

Overstory vegetation drives photosynthetically active radiation (PAR) levels at the surface of the floodplain terraces and in the stream channels. PAR levels, mediated by nutrient availability, determine the rates of primary productivity on the floodplain surface and in the stream channel. As such, a closed riparian forest canopy is less productive than a multi-level, diverse vegetation stature riparian floodplain plant assemblage of floodplain plants of diverse stature (Ecke et al., 2017). A mature, large-stature riparian plant assemblage only develops on a low disturbance, stable floodplain surface which, in turn, exists when channel migration and braiding rates are minimal. However, channel migration and braiding rates are reduced by processes that stabilize channel location, such as incision and deep, strong plant root growth (Hawley & MacMannis, 2019). Thus, a maximally productive riparian plant assemblage is one with a range of height and structure that tolerates disturbance due to channel migration and formation. But, beaver are also a key structuring agent for floodplain plants (Johnson et al., 2019; Westbrook, 2021). Beaver browse pressure selects for riparian plant species that tolerate the removal of stems, sprouts, or branches. Many browse-adapted plant species are more productive under browse pressure than not. Thus, beavers strongly alter stream and floodplain hydraulics through the digging of beaver canals, tunnels and burrows, and the constructions of dams, food caches, and lodges (G. A. Hood & Larson, 2015).

4.5 | Ecosystem services

Should we entrust a large rodent with such critical environmental engineering tasks? If restoring riverscapes is really such an important piece of our national climate action plan, should not we do it ourselves? Ultimately, the scale of changes that need to occur are beyond what we can accomplish and maintain on our own. However, beaver-based riverscape restoration has a high return on investment in both revenue and expense control (Baldwin, 2015; Blackfeet Nation, 2018; Blackfeet Nation & Levitus, 2019; Pollock et al., 2015; S. Thompson et al., 2021; Wheaton et al., 2019). Revenue generation typically results from increased tourism and outdoor recreation (e.g., hunting, fishing, hiking, camping, wildlife viewing), while expense reduction from lower expenditures in disaster mitigation, carbon management, water quality assurance, and water conservation. These ecosystem services by beaver, as well as many others not

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

discussed in detail here, is estimated at $69,000 per square kilometer, per year (S. Thompson et al., 2021). Secondary economic benefits of utilizing beaver coexistence and beaver mimicry in riverscape restoration would help offset the already low cost of implementing beaver mimicry and managing human–beaver conflict (Boyles & Savitzky, 2009).

4.6 | Overcoming institutional constraints to beaver-based restoration

Our fish, water, and forests depend on our willingness to act. We cannot just continue to study the situation without also taking action. There is absolutely more research that needs to be done to optimize and quantify beaver-based restoration impacts across all spatial and temporal scales. In an ideal world, we could wait to act until every last detail was sorted out. However, given the trajectory of climate change and increasingly threatened water resources we simply do not have that kind of time. Thus, we should implement, and continue to study, process-based methods in degraded streams across the continent, now. We should start rewriting our beaver management policies today to actively support coexistence over lethal management so that if and when beavers arrive in a riverscape they can thrive. We should proactively educate wildlife managers, land managers, and the public about the incredible value that these ecosystem engineers bring to our communities. Science and practice can, and should, go hand-in-hand.

There are certainly barriers that stand in the way of implementing beaver-based restoration. In the United States, high-level economic questions linger about the legality of water rights on beaver-impacted streams and the economics of stream restoration credits and whether beaver-created wetlands would count toward those. On a more fundamental sociocultural level, landowners worry that beavers will cut down all the trees, flood the roads, introduce waterborne diseases, and eat threatened fishes if they are allowed to recolonize streams. Some of these worries are founded in reality, for example, beavers do cut down trees, but they will not cut down all of them and there are non-lethal management strategies like wire-wrapping to protect important trees. However, some of these worries are founded in myth, for example, beavers are herbivores and do not eat fish. Understanding the conflicts—both real and perceived—between beavers, humans, and human infrastructure is a critical step for successfully developing and promoting effective coexistence strategies (Auster et al., 2019; Auster et al., 2021; Auster et al., 2022; Charnley et al., 2020; McKinstry & Anderson, 1999; Siemer et al., 2013). Continued education and outreach efforts are key to incentivize beaver-based restoration work (Morzillo & Needham, 2015).

Questions linger on the physical and ecological impacts of beaver-based restoration as well. For example, it is not entirely clear whether the impacts of beaver-based restoration will produce a linear or nonlinear response in the landscape when done at larger scales than researchers have previously examined. The different configurations and constructions of BDAs are still being tested and compared against one another (Davis et al., 2021; Munir & Westbrook, 2020), and more research is needed to determine the optimal configurations for a specific site. There is no clear consensus on how to maximize the chances of success when performing beaver relocation—how to live-trap the beavers, how long to quarantine them, whether or not the relocation site is intentionally prepared or not, if the impacts of relocated beavers versus in situ beavers differ, are all important considerations, with relatively little rigorous research published in the scientific literature (Dittbrenner et al., 2018; McCreesh et al., 2019; McKinstry et al., 2001). These unknowns are valid, but they should not completely paralyze beaver-based river restoration efforts. Not every stream will have these issues, and not every project needs to achieve fully optimized maximum restoration on the first attempt. Small restoration gains are better than no restoration gains, and from a precautionary, risk mitigating perspective, incremental progress has enormous value. Focusing beaver-based restoration efforts on streams and rivers with the lowest potential for human conflict and highest potential for restoration gains is a prudent path forward. There are so many streams and rivers that need restoration—it will take time to complete just the simplest, most straightforward projects. But, as projects progress, more data can and will be collected to inform future projects. This is the nature of science and land management in general, and applying this philosophy to beaver-based restoration is not a radical idea.

5 | CONCLUSION: WE NEED (NATURE'S) ENGINEERS

To return the full process-based functionality of connected floodplain systems we must acknowledge the critical role that biological components play—particularly beaver. When we remove beaver from streams and rivers, or prevent them from re-establishing in their ancestral watersheds, the stream-floodplain system falls into disrepair (Wohl, 2021b). Once they are disconnected from their floodplain, down-cut, incised streams simplify into single-threaded channels.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sediment and carbon are exported from long-term storage, water warms and becomes eutrophic, the landscape dries out and fires run for miles across a uniform expanse of fuel, all leaving little in the way of healthy habitat for fish and wildlife. But, beaver managed floodplains are biodiversity hotspots because beaver ponds and wetlands serve as sinks for carbon, processing centers for nitrogen and phosphorus, reservoirs for the storage and cooling of water, and mitigation sites for both drought and flooding. Thus, it is imperative that we foster beaver-dominated areas for the many services they provide.

We need to apply our knowledge of the physical and biological processes of functioning riverscapes and the role that beavers play to drive rapid, comprehensive, and durable action. Actions that address the pervasive degradation of North America's streams, rivers, and floodplains. Actions that rebuild the natural, functioning dynamics of riverscapes to permit robust responses to disturbance. Riverscape restoration, and in particular process-led and beaver-based restoration, should be the foundation of our national freshwater climate action plan.

ACKNOWLEDGMENTS

This Perspectives has benefited greatly from review and comments provided by Ben Goldfarb, Nick Bouwes, Martha Otis, Lisa Crozier, Shallin Busch, Alan Puttock, and three anonymous peer reviewers.

CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Chris E. Jordan: Conceptualization (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal). **Emily Fairfax:** Conceptualization (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Chris E. Jordan https://orcid.org/0000-0002-1557-3624
Emily Fairfax https://orcid.org/0000-0001-8480-1777

RELATED WIREs ARTICLES

Beaver: Nature's ecosystem engineers

REFERENCES

Albert, S., & Trimble, T. (2000). Beavers are partners in riparian restoration on the Zuni Indian Reservation. *Ecological Restoration*, *18*(2), 87–92 http://www.jstor.org/stable/43440851

Alongi, D. M. (2008). Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, *76*(1), 1–13.

Amlin, N. M., & Rood, S. B. (2003). Drought stress and recovery of riparian cottonwoods due to water table alteration along Willow Creek, Alberta. *Trees*, *17*, 351–358.

Anderson, N. L., Paszkowski, C. A., & Hood, G. A. (2015). Linking aquatic and terrestrial environments: Can beaver canals serve as movement corridors for pond-breeding amphibians? *Animal Conservation*, *18*, 287–294.

Appling, A. P., Bernhardt, E. S., & Stanford, J. A. (2014). Floodplain biogeochemical mosaics: A multidimensional view of alluvial soils. *Journal of Geophysical Research: Biogeosciences*, *119*(8), 1538–1553.

Auster, R. E., Barr, S. W., & Brazier, R. E. (2021). Improving engagement in managing reintroduction conflicts: Learning from beaver reintroduction. *Journal of Environmental Planning and Management*, *64*(10), 1713–1734. https://doi.org/10.1080/09640568.2020.1837089

Auster, R. E., Barr, S. W., & Brazier, R. E. (2022). Renewed coexistence: Learning from steering group stakeholders on a beaver reintroduction project in England. *European Journal of Wildlife Research*, *68*, 1. https://doi.org/10.1007/s10344-021-01555-6

Auster, R. E., Puttock, A., & Brazier, R. (2019). Unravelling perceptions of Eurasian beaver reintroduction in Great Britain. *Area*, *52*, 364–375. https://doi.org/10.1111/area.12576

Baldwin, J. (2015). Potential mitigation of and adaptation to climate-driven changes in California's highlands through increased beaver populations. *California Fish and Game*, *101*(4), 218–240.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Beechie, T. J., Imaki, H., Greene, J., Wade, A. A., Wu, H., Pess, G. R., Roni, P., Kimball, J. S., Stanford, J. A., Kiffney, P. M., & Mantua, N. J. (2013). Restoring salmon habitat for a changing climate. *River Research and Applications*, *29*(8), 939–960. https://doi.org/10.1002/rra.2590

Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., Roni, P., & Pollock, M. M. (2010). Process-based principles for restoring river ecosystems. *Bioscience*, *60*, 209–222.

Bellmore, J. R., & Baxter, C. V. (2014). Effects of geomorphic process domains on river ecosystems: A comparison of floodplain and confined valley segments. *River Research and Applications*, *30*(5), 617–630.

Blackfeet Nation. (2018). *Blackfeet climate change adaptation plan*. https://blackfeetclimatechange.com/our-environment/climate-change-adaptation-plan/

Blackfeet Nation, & Levitus, J. (2019). *The Ksik Stakii Project beaver mimicry guidebook*. https://bcapwebsite.files.wordpress.com/2019/12/beaver-mimicry-guidebook.pdf

Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., Wheaton, J. M., & Pollock, M. M. (2016). Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports*, *6*, 28581. https://doi.org/10.1038/srep28581

Boyles, S. L., & Savitzky, B. A. (2009). An analysis of the efficacy and comparative costs of using flow devices to resolve conflicts with North American beavers along roadways in the coastal plain of Virginia. In R. M. Timm & M. B. Madon (Eds.), *Proceedings of the 23rd Vertebrate Pest Conference* (Vol. 2008, pp. 47–52). University of California, Davis.

Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. L. (2021). Beaver: Nature's ecosystem engineers. *WIREs Water*, *8*(1), e1494 https://www.ncbi.nlm.nih.gov/pubmed/33614026

Briggs, M. A., Lautz, L. K., Hare, D. K., & González-Pinzón, R. (2013). Relating hyporheic fluxes, residence times, and redox-sensitive biogeochemical processes upstream of beaver dams. *Freshwater Science*, *32*(2), 622–641.

Burchsted, D., Daniels, M., Thorson, R., & Vokoun, J. (2010). The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *Bioscience*, *60*(11), 908–922.

Castro, J. M., & Thorne, C. R. (2019). The stream evolution triangle: Integrating geology, hydrology, and biology. *River Research and Applications*, *35*(4), 315–326.

Charnley, S., Gosnell, H., Davee, R., & Abrams, J. (2020). Ranchers and beavers: Understanding the human dimensions of beaver-related stream restoration on western rangelands. *Rangeland Ecology & Management*, *73*(5), 712–723.

Ciotti, D. C., McKee, J., Pope, K. L., Kondolf, G. M., & Pollock, M. M. (2021). Design criteria for process-based restoration of fluvial systems. *Bioscience*, *71*(8), 831–845.

Cluer, B., & Thorne, C. (2014). A stream evolution model integrating habitat and ecosystem benefits. *River Research and Applications*, *30*(2), 135–154.

Collins, B. D., Montgomery, D. R., Fetherston, K. L., & Abbe, T. B. (2012). The floodplain large-wood cycle hypothesis: A mechanism for the physical and biotic structuring of temperate forested alluvial valleys in the North Pacific coastal ecoregion. *Geomorphology*, *139–140*, 460–470.

Cornell, R., Andronescu, A., & Nguyen, K. (2011). *The effects of beaver dams on water quality and habitat*. Dept. of Earth and Atmospheric Sciences, Metropolitan State College of Denver.

Dame, R. F., & Patten, B. C. (1981). Analysis of energy flows in an intertidal oyster reef. *Marine Ecology Progress Series*, *5*(2), 115–124.

Dauwalter, D. C., & Walrath, J. D. (2018). Beaver dams, streamflow complexity, and the distribution of a rare minnow, *Lepidomeda copei*. *Ecology of Freshwater Fish.*, *27*, 606–616. https://doi.org/10.1111/eff.12374

Davee, R., Gosnell, H., & Charnley, S. (2019). *Using beaver dam analogues for fish and wildlife recovery on public and private rangelands in eastern Oregon* (Res. Pap. PNW-RP-612; pp. 29). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Davis, J., Lautz, L., Kelleher, C., Vidon, P., Russoniello, C., & Pearce, C. (2021). Evaluating the geomorphic channel response to beaver dam analog installation using unoccupied aerial vehicles. *Earth Surface Processes and Landforms*, *46*(12), 2349–2364.

Dittbrenner, B. J., Pollock, M. M., Schilling, J. W., Olden, J. D., Lawler, J. J., & Torgersen, C. E. (2018). Modeling intrinsic potential for beaver (Castor canadensis) habitat to inform restoration and climate change adaptation. *PLoS One*, *13*(2), e0192538 https://www.ncbi.nlm.nih.gov/pubmed/29489853

Ecke, F., Levanoni, O., Audet, J., Carlson, P., Eklöf, K., Hartman, G., McKie, B., Ledesma, J., Segersten, J., Truchy, A., & Futter, M. (2017). Meta-analysis of environmental effects of beaver in relation to artificial dams. *Environmental Research Letters*, *12*(11), 113002.

Environmental Law Institute (ELI). (2016). *Stream mitigation: Science, policy, and practice*. Environmental Law Institute https://www.eli.org/sites/default/files/eli-pubs/stream-mitigation-science-policy-and-practice-finalreport.pdf

Fairfax, E., & Small, E. E. (2018). Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape. *Ecohydrology*, *11*(7), 1–14. https://doi.org/10.1002/eco.1993

Fairfax, E., & Whittle, A. (2020). Smokey the beaver: Beaver-dammed riparian corridors stay green during wildfire throughout the western United States. *Ecological Applications*, *30*(8), 1–8.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes: A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *Bioscience*, *52*(6), 483–498. https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2

Feit, H. A. (1986). James Bay Cree Indian Management and Moral Considerations of Fur bearers. In *Native people and renewable resource management. 1986 symposium of the Alberta Society of Professional Biologists (ASPB)* (pp. 49–65). ASPB.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Finco, M., Quayle, B., Zhang, Y., Lecker, J., Megown, K. A., & Brewer, C. K. (2012). *Monitoring trends and burn severity (MTBS): Monitoring wildfire activity for the past quarter century using Landsat data*. Paper presented at the In: Morin, Randall S.; Liknes, Greg C. comps. Moving from status to trends: Forest Inventory and Analysis (FIA) symposium 2012; 2012 December 4–6; Baltimore, MD. Gen. Tech. Rep. NRS-P-105 (pp. 222–228). US Department of Agriculture, Forest Service, Northern Research Station [CD-ROM].

Foster, C. N., Banks, S. C., Cary, G. J., Johnson, C. N., Lindenmayer, D. B., & Valentine, L. E. (2020). Animals as agents in fire regimes. *Trends in Ecology & Evolution*, *35*(4), 346–356.

Fouty, S. C. (2018). *Euro-American beaver trapping and its long-term impact on drainage network form and function, water abundance, delivery, and system stability*. In Johnson, R., Carothers, S. W., Finch, D. M., Kingsley, K. J., Stanley, J. T. (Tech. eds.). Riparian research and management: Past, present, future: Volume 1. Gen. Tech. Rep. RMRS-GTR-377. USDA USFS Rocky Mountain Research Station (pp. 226). https://doi.org/10.2737/RMRS-GTR-377.

Gadgil, M., Berkes, F., & Folke, C. (1993). Indigenous knowledge for biodiversity conservation. *Ambio*, *22*(2), 151–156.

Goss, M., Swain, D. L., Abatzoglou, J. T., Sarhadi, A., Kolden, C. A., Williams, A. P., & Diffenbaugh, N. S. (2020). Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. *Environmental Research Letters*, *15*(9), 094016.

Hammerson, G. A. (1994). Beaver (*Castor canadensis*): Ecosystem alterations, management, and monitoring. *Natural Areas Journal*, *14*(1), 44–57.

Hawley, R. J., & MacMannis, K. R. (2019). Tree roots as a dominant agent of streambed habitat, profile pattern, and grade control. *Geomorphology*, *343*, 81–91.

Helton, A. M., Poole, G. C., Payn, R. A., Izurieta, C., & Stanford, J. A. (2014). Relative influences of the river channel, floodplain surface, and alluvial aquifer on simulated hydrologic residence time in a montane river floodplain. *Geomorphology*, *205*, 17–26 https://www.sciencedirect.com/science/article/pii/S0169555X12000189

Hood, G. A., & Bayley, S. E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, *141*(2), 556–567.

Hood, G. A., & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. *Freshwater Biology*, *60*(1), 198–208.

Hood, W. G. (2012). Beaver in tidal marshes: Dam effects on low-tide channel pools and fish use of estuarine habitat. *Wetlands*, *32*(3), 401–410.

Ives, R. L. (1942). The beaver-meadow complex. *Journal of Geomorphology*, *5*(3), 191–203.

Janzen, K., & Westbrook, C. J. (2011). Hyporheic flows along a channelled peatland: Influence of beaver dams. *Canadian Water Resources Journal*, *36*(4), 331–347.

Johnson, M. F., Thorne, C. R., Castro, J. M., Kondolf, G. M., Mazzacano, C. S., Rood, S. B., & Westbrook, C. (2019). Biomic river restoration: A new focus for river management. *River Research and Applications*, *36*(1), 3–12.

Kasprak, A., Hough-Snee, N., Beechie, T., Bouwes, N., Brierley, G., Camp, R., Fryirs, K., Imaki, H., Jensen, M., O'Brien, G., Rosgen, D., & Wheaton, J. (2016). The blurred line between form and process: A comparison of stream channel classification frameworks. *PLoS One*, *11*(3), e0150293.

Kauffman, J. B., Beschta, R. L., Otting, N., & Lytjen, D. (1997). An ecological perspective of riparian and stream restoration in the Western United States. *Fisheries*, *22*(5), 12–24.

Keeble-Toll, A. K. (2018). *Braiding pine: Weaving traditional knowledge, community need, and scientific method in Sierra Nevada meadow restoration*. https://ui.adsabs.harvard.edu/abs/2018AGUFMPA51C0784K

Kimmerer, R. W. (2000). Native knowledge for native ecosystems. *Journal of Forestry*, *98*(8), 4–9.

Kimmerer, R. W., & Lake, F. K. (2001). The role of indigenous burning in land management. *Journal of Forestry*, *99*(11), 36–41.

Klotz, R. L. (1998). Influence of beaver ponds on the phosphorus concentration of stream water. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1228–1235.

Klotz, R. L. (2010). Reduction of high nitrate concentrations in a Central New York state stream impounded by beaver. *Northeastern Naturalist*, *17*(3), 349–356.

Kroes, D. E., & Bason, C. W. (2015). Sediment-trapping by beaver ponds in streams of the mid-Atlantic Piedmont and coastal plain, USA. *Southeastern Naturalist*, *14*(3), 577–595.

Larsen, A., Larsen, J. R., & Lane, S. N. (2021). Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. *Earth-Science Reviews*, *218*, 103623.

Laurel, D., & Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, *44*(1), 342–353.

Lazar, J. G., Addy, K., Gold, A. J., Groffman, P. M., McKinney, R. A., & Kellogg, D. Q. (2015). Beaver ponds: Resurgent nitrogen sinks for rural watersheds in the northeastern United States. *Journal of Environmental Quality*, *44*(5), 1684–1693.

Lowry, M. M. (1993). *Groundwater elevations and temperature adjacent to a beaver pond in central Oregon* (Thesis). Dept. of Forest Engineering, Oregon State University.

Macfarlane, W. W., Wheaton, J. M., Bouwes, N., Jensen, M. L., Gilbert, J. T., Hough-Snee, N., & Shivik, J. A. (2015). Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*, *277*, 72–99.

Magilligan, F. J., Nislow, K. H., Fisher, G. B., Wright, J., Mackey, G., & Laser, M. (2008). The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA. *Geomorphology*, *97*(3–4), 467–482.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Majerova, M., Neilson, B. T., Schmadel, N. M., Wheaton, J. M., & Snow, C. J. (2015). Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. *Hydrology and Earth System Sciences Discussions*, *12*(1), 839–878.

Majerova, M., Neison, B. T., & Roper, B. B. (2020). Beaver dam influences on streamflow hydraulic properties and thermal regimes. *Science of the Total Environment*, *718*(134853), 1–14. https://www.sciencedirect.com/science/article/pii/S0048969719348454

Maret, T. J., Parker, M., & Fannin, T. E. (1987). The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming. *Water Research*, *21*(3), 263–268.

McCreesh, R. K., Fox-Dobbs, K., Wimberger, P., Woodruff, K., Holtgrieve, G., & Pool, T. K. (2019). Reintroduced beavers rapidly influence the storage and biogeochemistry of sediments in headwater streams (Methow River, Washington). *Northwest Science*, *93*(2), 112–121.

McKinstry, M. C., & Anderson, S. H. (1999). Attitudes of private-and public-land managers in Wyoming, USA, toward beaver. *Environmental Management*, *23*(1), 95–101.

McKinstry, M. C., Caffrey, P., & Anderson, S. H. (2001). The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association*, *37*(6), 1571–1577.

Morgan, L. H. (1868). *The American beaver and his works*. JB Lippincott.

Mori, A. S., & Johnson, E. A. (2013). Assessing possible shifts in wildfire regimes under a changing climate in mountainous landscapes. *Forest Ecology and Management*, *310*, 875–886.

Morzillo, A. T., & Needham, M. D. (2015). Landowner incentives and normative tolerances for managing beaver impacts. *Human Dimensions of Wildlife*, *20*(6), 514–530. https://doi.org/10.1080/10871209.2015.1083062

Munir, T. M., & Westbrook, C. J. (2020). Beaver dam analogue configurations influence stream and riparian water table dynamics of a degraded spring-fed creek in the Canadian Rockies. *River Research and Applications*, *37*(3), 330–342.

Muskopf, S. A. (2007). *The effect of beaver (Castor canadensis) dam removal on total phosphorus concentration in Taylor Creek and wetland, South Lake Tahoe*. Humboldt State University.

Naiman, R. J., Decamps, H., & McClain, M. E. (2010). *Riparia: Ecology, conservation, and management of streamside communities*. Elsevier.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American streams by beaver. *Bioscience*, *38*(11), 753–762.

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, *67*(5), 1254–1269.

Nash, C. S., Grant, G. E., Charnley, S., Dunham, J. B., Gosnell, H., Hausner, M. B., Pilliod, D. S., & Taylor, J. D. (2021). Great expectations: Deconstructing the process pathways underlying beaver-related restoration. *Bioscience*, *71*(3), 249–267. https://doi.org/10.1093/biosci/biaa165

Nash, C. S., Selker, J. S., Grant, G. E., Lewis, S. L., & Noël, P. (2018). A physical framework for evaluating net effects of wet meadow restoration on late-summer streamflow. *Ecohydrology*, *11*(5), e1953.

Neff, D. J. (1957). Ecological effects of beaver habitat abandonment in the Colorado Rockies. *The Journal of Wildlife Management*, *21*(1), 80–84.

Nummi, P., Liao, W., van der Schoor, J., & Loehr, J. (2021). Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation*, *30*(10), 2655–2670.

Nummi, P., Vehkaoja, M., Pumpanen, J., & Ojala, A. (2018). Beavers affect carbon biogechemistry: Both short-term and long-term processes are involved. *Mammal Review*, *48*(4), 298–311. https://doi.org/10.1111/mam.12134

Osei, N. A., Gurnell, A. M., & Harvey, G. L. (2015). The role of large wood in retaining fine sediment, organic matter and plant propagules in a small, single-thread forest river. *Geomorphology*, *235*, 77–87.

Pearce, C., Vidon, P., Lautz, L., Kelleher, C., & Davis, J. (2021a). Impact of beaver dam analogues on hydrology in a semi-arid floodplain. *Hydrological Processes*, *35*(7), e14275. https://doi.org/10.1002/hyp.14275

Pearce, C., Vidon, P., Lautz, L., Kelleher, C., & Davis, J. (2021b). Short-term impact of beaver dam analogues on streambank erosion and deposition in semi-arid landscapes of the western USA. *River Research and Applications*, *37*(7), 1032–1037.

Pethick, J. (1992). Saltmarsh geomorphology. In *Saltmarshes: Morphodynamics, conservation and engineering significance* (pp. 41–62). Cambridge, England: Cambridge University Press.

Phillips, J. D. (2016). Landforms as extended composite phenotypes. *Earth Surface Processes and Landforms*, *41*(1), 16–26.

Pilliod, D. S., Rohde, A. T., Charnley, S., Davee, R. R., Dunham, J. B., Gosnell, H., Grant, G. E., Hausner, M. B., Huntington, J. L., & Nash, C. (2017). Survey of beaver-related restoration practices in rangeland streams of the Western USA. *Environmental Management*, *61*(1), 58–68. https://doi.org/10.1007/s00267-017-0957-6

Pollock, M. M., Beechie, T. J., & Jordan, C. E. (2007). Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms*, *32*(8), 1174–1185.

Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *Bioscience*, *64*(4), 279–290.

Pollock, M. M., Castro, J., Jordan, C. E., Lewallen, G., & Woodruff, K. (2015). *The beaver restoration guidebook: Working with beaver to restore streams, wetlands, and floodplains* (Version 1.02) (p. 189). United States Fish and Wildlife Service.

Pollock, M. M., Naiman, R. J., Erickson, H. E., Johnston, C. A., Pastor, J., & Pinay, G. (1995). Beaver as engineers—Influences on biotic and abiotic characteristics of drainage basins. *Linking Species & Ecosystems*, 117–126. Boston, MA: Springer. https://doi.org/10.1007/978-1-4615-1773-3

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Pollock, M. M., Pess, G., & Beechie, T. J. (2004). The importance of beaver ponds to Coho Salmon production in the Stillaguamish River basin, Washington, USA. *North American Journal of Fisheries Management*, *24*, 749–760.

Poole, G. C., O'Daniel, S. J., Jones, K. L., Woessner, W. W., Bernhardt, E. S., Helton, A. M., Stanford, J. A., Boer, B. R., & Beechie, T. J. (2008). Hydrologic spiralling: The role of multiple interactive flow paths in stream ecosystems. *River Research and Applications*, *24*(7), 1018–1031. https://doi.org/10.1002/rra.1099

Puttock, A., Graham, H. A., Ashe, J., Luscombe, D. J., & Brazier, R. E. (2021). Beaver dams attenuate flow: A multi-site study. *Hydrological Processes*, *35*(2), e14017 https://www.ncbi.nlm.nih.gov/pubmed/33678948

Puttock, A., Graham, H. A., Carless, D., & Brazier, R. E. (2018). Sediment and nutrient storage in a beaver engineered wetland. *Earth Surface Processes and Landforms*, *43*, 2358–2370. https://doi.org/10.1002/esp.4398

Puttock, A., Graham, H. A., Cunliffe, A. M., Elliott, M., & Brazier, R. E. (2017). Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of the Total Environment*, *576*, 430–443 https://www.ncbi.nlm.nih.gov/pubmed/27792958

Robinson, C. T., Schweizer, P., Larsen, A., Schubert, C. J., & Siebers, A. R. (2020). Beaver effects on macroinvertebrate assemblages in two streams with contrasting morphology. *Science of the Total Environment*, *722*, 137899.

Romansic, J. M., Nelson, N. L., Moffett, K. B., & Piovia-Scott, J. (2021). Beaver dams are associated with enhanced amphibian diversity via lengthened hydroperiods and increased representation of slow-developing species. *Freshwater Biology*, *66*(3), 481–494. https://doi.org/10.1111/fwb.13654

Rosell, F., Bozser, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, *35*(3), 248–276.

Ruedemann, R., & Schoonmaker, W. J. (1938). Beaver dams as geologic agents. *Science*, *88*(2292), 523–525.

Sands, A., & Howe, G. (1977). Riparian forests in California, their ecology and conservation. Paper presented at the Importance, Preservation and Management of Riparian Habitat: A Symposium, Tuscon, AZ.

Scamardo, J., & Wohl, E. (2020). Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado front range, USA. *River Research and Applications*, *36*(3), 398–409.

Seton, E. T. (1929). *Lives of game animals* (Vol. 4, pp. 441–501). Doubleday, Doran and Co.

Shepherd, N. L., & Nairn, R. W. (2020). Metals retention in a net alkaline mine drainage impacted stream due to the colonization of the North American beaver (*Castor canadensis*). *Science of the Total Environment*, *731*, 139203.

Shepherd, N. L., & Nairn, R. W. (2021). Induced mobilization of stored metal precipitates from beaver (*Castor canadensis*) created wetlands on a mine drainage impacted stream. *Wetlands Ecology and Management*, *30*, 127–137.

Sherriff, L. (2021). *Beaver believers: Native Americans promote resurgence of 'nature's engineers'*. The Guardian.

Short, L. E., Gabet, E. J., & Hoffman, D. F. (2015). The role of large woody debris in modulating the dispersal of a post-fire sediment pulse. *Geomorphology*, *246*, 351–358.

Siemer, W. F., Jonker, S. A., Decker, D. J., & Organ, J. F. (2013). Toward an understanding of beaver management as human and beaver densities increase. *Human-Wildlife Interactions*, *7*(1), 114–131.

Silverman, N. L., Allred, B. W., Donnelly, J. P., Chapman, T. B., Maestas, J. D., Wheaton, J. M., & White, J. (2019). Low-tech riparian and wet meadow restoration increases vegetation productivity and resilience across semiarid rangelands. *Restoration Ecology*, *27*(2), 269–278. https://doi.org/10.1111/rec.12869

Skidmore, P., & Wheaton, J. M. (2022). Natural infrastructure—Can restored riverscapes help us adapt to climate change. *Anthropocene*. https://doi.org/10.13140/RG.2.2.33525.86248

Snodgrass, J. W., & Meffe, G. K. (1998). Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. *Ecology*, *79*(3), 928–942.

Stella, J. C., Hayden, M. K., Battles, J. J., Piégay, H., Dufour, S., & Fremier, A. K. (2011). The role of abandoned channels as refugia for sustaining pioneer riparian forest ecosystems. *Ecosystems*, *14*(5), 776–790.

Stott, P. (2016). How climate change affects extreme weather events. *Science*, *352*(6293), 1517–1518.

Stringer, A. P., & Gaywood, M. J. (2016). The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, *46*(4), 270–283.

Swain, D. L. (2021). A shorter, sharper rainy season amplifies California wildfire risk. *Geophysical Research Letters*, *48*(5), 1–5.

Thompson, D. M., & Stull, G. N. (2002). The development and historic use of habitat structures in channel restoration in the United States: The grand experiment in fisheries management. *Géographie Physique et Quaternaire*, *56*(1), 45–60.

Thompson, S., Vehkaoja, M., Pellikka, J., & Nummi, P. (2021). Ecosystem services provided by beavers *Castor* spp. *Mammal Review*, *51*(1), 25–39.

USEPA. (2013). *National rivers and streams assessment 2013–2014: A collaborative survey* (EPA-841-R-19-001).

Viles, H. A. (1988). *Biogeomorphology: B.* Blackwell.

Vivian, L. M., Godfree, R. C., Colloff, M. J., Mayence, C. E., & Marshall, D. J. (2014). Wetland plant growth under contrasting water regimes associated with river regulation and drought: Implications for environmental water management. *Plant Ecology*, *215*(9), 997–1011.

Wade, J., Lautz, L., Kelleher, C., Vidon, P., Davis, J., Beltran, J., & Pearce, C. (2020). Beaver dam analogues drive heterogeneous groundwater–surface water interactions. *Hydrological Processes*, *34*(26), 5340–5353.

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Wang, C., Smolders, S., Callaghan, D. P., van Belzen, J., Bouma, T. J., Hu, Z., Wen, Q., & Temmerman, S. (2020). Identifying hydro-geomorphological conditions for state shifts from bare tidal flats to vegetated tidal marshes. *Remote Sensing*, *12*(14), 2316. https://doi.org/10.3390/rs12142316

Wang, X., Shaw, E. L., Westbrook, C. J., & Bedard-Haughn, A. (2018). Beaver dams induce hyporheic and biogeochemical changes in riparian areas in a mountain peatland. *Wetlands*, *38*(5), 1017–1032.

Wathen, G., Allgeier, J. E., Bouwes, N., Pollock, M. M., Schindler, D. E., & Jordan, C. E. (2019). Beaver activity increases habitat complexity and spatial partitioning by steelhead trout. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(7), 1086–1095.

Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., Wirtz, J., & Jordan, C. E. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS One*, *12*(5), e0176313 https://www.ncbi.nlm.nih.gov/pubmed/28520714

Wegener, P., Covino, T., & Wohl, E. E. (2017). Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. *Water Resources Research*, *53*, 4606–4623.

Weigelhofer, G., Hein, T., & Bondar-Kunze, E. (2018). Phosphorus and nitrogen dynamics in riverine systems: Human impacts and management options. In S. Schmutz & J. Sendzimir (Eds.), *Riverine ecosystem management: Aquatic ecology series 8*. Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-73250-3_10

Weirich, J. J. (2021). *Beaver moderated fire resistance in the north cascades and potential for climate change adaptation* (Masters thesis collection 660). Eastern Washington University. https://dc.ewu.edu/theses/660

Westbrook, C. J. (2021). Beaver as agents of plant disturbance. In *Plant disturbance ecology* (pp. 489–528). Elsevier.

Westbrook, C. J., Ronnquist, A., & Bedard-Haughn, A. (2020). Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm. *Hydrological Processes*, *34*(18), 3726–3737.

Westbrook, C. J., Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain Riparian area. *Water Resources Research*, *42*(6), 06404. https://doi.org/10.1029/2005WR004560

Wheaton, J. M., Bennett, S. N., Bouwes, N. W., Maestas, J. D., & Shahverdian, S. M. (2019). *Low-tech process-based restoration of Riverscapes: Design manual*. Utah State University Restoration Consortium.

Whipple, A. (2019). *Riparian resilience in the face of interacting disturbances: Understanding complex interactions between wildfire, erosion, and beaver (*Castor canadensis*) in grazed dryland riparian systems of low order streams in North Central Washington State, USA* (Masters thesis collection 586). Eastern Washington University.

Williams, A. P., Abatzoglou, J. T., Gershunov, A., Guzman-Morales, J., Bishop, D. A., Balch, J. K., & Lettenmaier, D. P. (2019). Observed impacts of anthropogenic climate change on wildfire in California. *Earth's Future*, *7*(8), 892–910.

Williams, J. (2013). Exploring the onset of high-impact mega-fires through a forest land management prism. *Forest Ecology and Management*, *294*, 4–10.

Wohl, E. (2013). Landscape-scale carbon storage associated with beaver dams. *Geophysical Research Letters*, *40*(14), 3631–3636.

Wohl, E. (2021a). An integrative conceptualization of floodplain storage. *Reviews of Geophysics*, *59*(2), e2020RG000724.

Wohl, E. (2021b). Legacy effects of loss of beavers in the continental United States. *Environmental Research Letters*, *16*(2), 025010.

Wohl, E., Castro, J., Cluer, B., Merritts, D., Powers, P., Staab, B., & Thorne, C. (2021). Rediscovering, reevaluating, and restoring lost river-wetland corridors. *Frontiers in Earth Science*, *9*, 511.

Wohl, E., Lininger, K. B., & Scott, D. N. (2017). River beads as a conceptual framework for building carbon storage and resilience to extreme climate events into river management. *Biogeochemistry*, *141*(3), 365–383.

Wohl, E., Marshall, A. E., Scamardo, J., White, D., & Morrison, R. R. (2022). Biogeomorphic influences on river corridor resilience to wildfire disturbances in a mountain stream of the Southern Rockies, USA. *Science of the Total Environment*, *820*, 153321.

Yousaf, A., Khalid, N., Aqeel, M., Noman, A., Naeem, N., Sarfraz, W., Ejaz, U., Qaiser, Z., & Khalid, A. (2021). Nitrogen dynamics in wetland systems and its impact on biodiversity. *Nitrogen*, *2*, 196–217. https://doi.org/10.3390/nitrogen2020013

How to cite this article: Jordan, C. E., & Fairfax, E. (2022). Beaver: The North American freshwater climate action plan. *WIREs Water*, *9*(4), e1592. https://doi.org/10.1002/wat2.1592

20491948, 2022, 4, Downloaded from https://wires.onlinelibrary.wiley.com/doi/10.1002/wat2.1592, Wiley Online Library on [15/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

CHAPTER EIGHT

Nesting Success and Resource Selection of Greater Sage-Grouse

Nicholas W. Kaczor, Kent C. Jensen, Robert W. Klaver, Mark A. Rumble, Katie M. Herman-Brunson, and Christopher C. Swanson

Abstract. Declines of Greater Sage-Grouse (*Centrocercus urophasianus*) in South Dakota are a concern because further population declines may lead to isolation from populations in Wyoming and Montana. Furthermore, little information exists about reproductive ecology and resource selection of sage grouse on the eastern edge of their distribution. We investigated Greater Sage-Grouse nesting success and resource selection in South Dakota during 2006–2007. Radiomarked females were tracked to estimate nesting rates, nest success, and habitat resources selected for nesting. Nest initiation was 98.0%, with a maximum likelihood estimate of nest success of 45.6 ± 5.3%. Females selected nest sites that had greater sagebrush canopy cover and visual obstruction of the nest bowl compared to random sites. Nest survival models indicated that taller grass surrounding nests increased nest survival. Tall grass may supplement the low sagebrush cover in this area in providing suitable nest sites for Greater Sage-Grouse. Land managers on the eastern edge of Greater Sage-Grouse range could focus on increasing sagebrush density while maintaining tall grass by developing range management practices that accomplish this goal. To achieve nest survival rates similar to other populations, predictions from our models suggest 26 cm grass height would result in approximately 50% nest survival. Optimal conditions could be accomplished by adjusting livestock grazing systems and stocking rates.

Key Words: Centrocercus urophasianus, Greater Sage-Grouse, nest initiation, nest success, renesting, resource selection, sagebrush, South Dakota.

Kaczor, N. W., K. C. Jensen, R. W. Klaver, M. A. Rumble, K. M. Herman-Brunson, and C. C. Swanson. 2011. Nesting success and resource selection of Greater Sage-Grouse. Pp. 107–118 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage grouse) are a sensitive species for state and federal resource management agencies due to declining populations and degradation and loss of nesting habitat (Aldridge and Brigham 2001, Connelly et al. 2004, Schroeder et al. 2004). Estimated trends of male sage grouse lek counts in South Dakota declined steadily from 1973 to 1997. From 1997 to 2004, sage grouse populations may have increased slightly (Connelly et al. 2004). Isolation from populations in neighboring states raises additional concerns for sage grouse persistence in South Dakota (Aldridge et al. 2008).

Declines in sage grouse populations have resulted in several petitions to list sage grouse under the Endangered Species Act (ESA) of 1973 (Connelly et al. 2004). Currently, federal land management agencies are responsible for approximately 66% of the sagebrush landscape in the United States. Federal agencies such as the U.S. Bureau of Land Management (BLM) and U.S. Forest Service (USFS) are directed by administrative policy to manage public lands for sustained multiple use under the Federal Land Policy and Management Act (1976) and the Public Rangelands Improvement Act (1978). Currently, sage grouse are managed as a sensitive species by BLM and USFS, and their management should not result in further population declines of sage grouse, which could lead to listing under ESA. The South Dakota Department of Game, Fish, and Parks has identified sage grouse as a species of special concern (South Dakota Department of Game, Fish, and Parks 2006). Listing of sage grouse under the ESA could have major ramifications on the use and management of public lands in the western United States (Knick et al. 2003).

Nest success is one factor that can determine whether sage grouse populations increase or decrease (Braun 1998, Schroeder et al. 1999, Dinsmore and Johnson 2005). Yet information is lacking on the ecological requirements of nesting sage grouse in western South Dakota. The objectives of this study were to develop an understanding on the nesting ecology, success, and resource selection of sage grouse at the eastern edge of their range.

STUDY AREA

The study was conducted within a 3,500 km^2 area in Butte and Harding counties, South Dakota; Crook County, Wyoming; and Carter County, Montana (44°44′ N to 45°20′ N, 103°15′ W to 104°21′ W; Fig. 8.1). Approximately 75% of the area was privately owned. The remaining 25% of the study area was managed by the BLM and State of South Dakota School and Public Lands Division. The area was predominately used for grazing, although small grain production also occurred. Open-pit mining for bentonite occurred at the south end of the study site on Pierre soils (C. Berdan, pers. comm.).

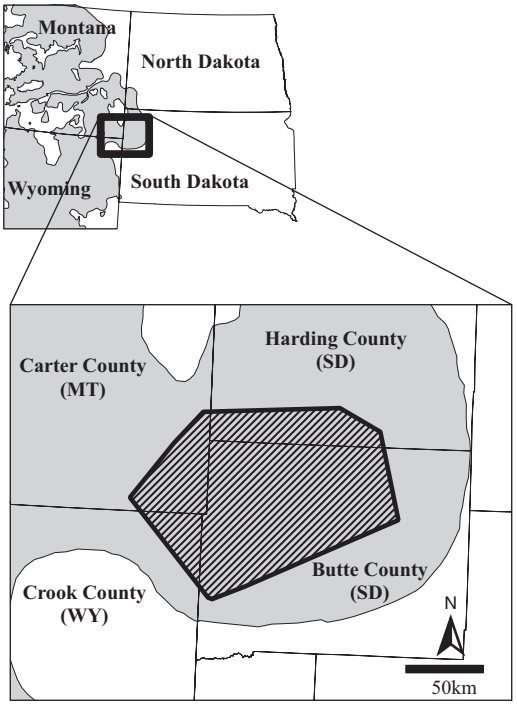


Figure 8.1. Location of study area for Greater Sage-Grouse in Butte, Carter, Crook, and Harding counties, 2006–2007. The hatched area encompasses all locations; the gray area is the current range of Greater Sage-Grouse (Schroeder et al. 2004).

Vegetation consisted of short shrubs, mostly Wyoming big sagebrush (*Artemisia tridentata* spp.) and plains silver sagebrush (*A. cana* spp.). Other shrubs included broom snakeweed (*Gutierrezia sarothrae*), greasewood (*Sarcobatus vermiculatus*), and saltbushes (*Atriplex* spp.) (Johnson and Larson 1999). Common grasses included western wheatgrass (*Pascopyrum smithii*), Junegrass (*Koeleria macrantha*), bluegrass species (*Poa* spp.), green needle-grass (*Nassella viridula*), and Japanese brome (*Bromus japonicus*). Common forbs included western yarrow (*Achillea millefolium*), common dandelion (*Taraxacum officinale*), pepperweed (*Lepidium*

densiflorum), and field pennycress (*Thlaspi arvense*) (Johnson and Larson 1999).

Temperatures in summer (May–August) averaged 20.1°C but can reach highs of 43.3°C (South Dakota State Climate Office 2007). During the months of March through June 2006 and 2007, the study area received approximately 14 cm and 22 cm of precipitation, 33% less and 5% more than the 58-year average of 21 cm (1956–2007; South Dakota State Climate Office 2007). Elevation ranges from 840 to 1,225 m above sea level with nearly level to moderately steep clayey soils over clay shale (Johnson 1976).

METHODS

Data Collection

We captured female sage grouse at or near six leks using large nets and spotlighting them from all-terrain vehicles each year between March and mid-April 2006 and 2007 (Giesen et al. 1982, Wakkinen et al. 1992). Females were weighed and equipped with a 22-g necklace-style transmitter; transmitters were approximately 1.4% of mean female sage grouse body mass and had a life expectancy of 434 days. Transmitters could be detected from a distance of approximately 2–5 km from the ground and were equipped with an 8-hour mortality switch. Females were classified as yearlings (<1 yr old) or adults (>1 yr old) based on primary wing feather characteristics (Eng 1955, Crunden 1963). The South Dakota State University Institutional Animal Care and Use Committee approved trapping and handling techniques, as well as study design (Protocol #07-A032).

We located radio-marked female sage grouse twice each week during the breeding, laying, and incubation periods. In the event we could not locate an individual from the ground, we searched the study area from a fixed-wing aircraft to obtain an approximate location. Once a female was believed to be incubating, we recorded four coordinates approximately 15 m away from the nest in the four cardinal directions with a Global Positioning System (GPS) receiver. We confirmed nest presence/absence during the subsequent visit. If a female was present on the second visit, we flushed her to determine clutch size. Our use of this method did not decrease nest survival for the immediate interval after the female was flushed from the nest. Nests were considered successful if ≥1 egg hatched. We calculated distances from nearest active display ground to nests, renests, and previous nests by the same bird using Hawth's Analysis Tool (Beyer 2004).

We characterized vegetation at nest sites after their fate was determined. Four 50-m transects were established radiating in the four cardinal directions from the nest bowl and four additional 5 m transects were established at the 45° intervals. A modified Robel pole was used to estimate visual obstruction (VOR) and maximum grass height at 1-m intervals from 0 m to 5 m ($n = 21$), and at 10-m intervals out to 50 m ($n = 20$) along each 50 m transect (Robel et al. 1970, Benkobi et al. 2000). We estimated sagebrush (*A. tridentata* spp. and *A. cana* spp.) density and height at 10-m intervals ($n = 80$) using the point-centered quarter method (Cottam and Curtis 1956). Vegetation canopy cover was estimated using a 0.10 m^2 quadrat at 1-m intervals to 5 m ($n = 44$) and at 2-m intervals along the long transects to 30 m ($n = 52$). We estimated percent canopy cover for total vegetation, grass, forb, shrub, litter, bare ground, and individual shrub and grass species (Daubenmire 1959). This method is amenable to collecting data on windy days and yields data that are similar (<3% difference for sagebrush) to the line-intercept method, but may provide more accurate estimates of cover (Floyd and Anderson 1987, Booth et al. 2006).

We measured an equal number of random sites within a 3-km buffer of capture leks to estimate resource selection. We navigated to the coordinates of random sites with a GPS and located the center of the transects over the nearest sagebrush because sage grouse usually nest beneath a shrub.

Data Analyses

Nesting Parameters

We used the multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test the null hypothesis that there were no differences between mass of female age-classes, clutch size of female age-classes, clutch size between first nests and renests, nest initiation date between years, distance among nests within a year, distance between nests between years (nest site fidelity), and distance to display grounds between years and age-classes of females. To avoid biasing estimates of nesting and renesting rates, we randomly

selected one observation for females that nested both years. Chi-square goodness-of-fit tests were used to test for differences in nest initiation rates between years and between age-classes of females. Statistical significance was set at $\alpha \leq 0.05$. Egg hatchability was the proportion of eggs hatching from successful clutches.

Average grass height and VOR were calculated for each 1-m interval away from the nest to 5 m, at 10-m intervals from 10 to 50 m, and for the site at 0 to 50 m. We used a maximum likelihood estimator to estimate sagebrush density (Pollard 1971). We calculated average sagebrush height for each site from the sagebrush plants that were measured to estimate density. Canopy coverage values were recoded to midpoint values of categories, and these were summarized to an average for 0 to 5 m, 6 to 30 m, and for the site at 0 to 30 m (Daubenmire 1959). To reduce the number of variables in the vegetative dataset to a manageable level and identify biologically important variables to carry forward in the analyses, we used MRPP to identify variables that exhibited differences ($\alpha \leq 0.15$) between nest and random sites, and again between successful and failed nests (Boyce et al. 2002, Stephens et al. 2005). Two separate screen processes were conducted as some variables could be important for nest selection but may not have a measurable effect on nest success.

Resource Selection

We identified ten habitat variables from the nest site selection MRPP analyses (Table 8.1). We used these and a year effect to investigate sage grouse nesting resource selection. Variables included: percent total vegetation cover, grass cover, sagebrush cover, and litter; site averages for sagebrush height, grass height, and visual obstruction; grass height 0–5 m from the nest; visual obstruction at the nest; and visual obstruction 1 m from nest.

Year was included as a design variable in all resource selection candidate models. To reduce potential variable interaction in our models, variables that were correlated to one another ($r > 0.70$) were not included in the same model (e.g., total vegetation cover plus grass cover). We used an information theoretic approach with logistic regression to estimate the support for models evaluating resource selection at nest sites (Burnham and Anderson 2002, SAS Institute Inc. 2007). Due to a small sample size with respect to the number of parameters estimated ($n/K < 40$); we used the small-sample adjustment for Akaike's Information Criterion (AIC_c) to evaluate models (Burnham and Anderson 2002). We ranked our models based on differences between AIC_c for each model and the minimum AIC_c model (ΔAIC_c), and Akaike weights (w_i) to assess the weight of evidence in favor of each model and the sum AIC_c weight for each variable (Beck et al. 2006). In addition, we investigated the slope of the coefficient estimates (β) to determine variable effect. We evaluated the predictive strength of our models using a receiver operation characteristic curve (ROC); values between 0.7 and 0.8 were considered acceptable predictive discrimination and values higher than 0.8 were considered excellent predictive discrimination. Model goodness-of-fit was determined using a Hosmer–Lemeshow test (Hosmer and Lemeshow 2000).

Nest Success

We used the nest survival procedure in program MARK to evaluate environmental and biological factors that might influence nest survival (White and Burnham 1999, Dinsmore et al. 2002). We standardized nesting dates among years by using the earliest date we discovered a nest as the first day of the nesting season. We monitored nests over a 59-day period beginning 23 April and ending 20 June, which comprised 58 daily intervals of observations to be used in estimating daily survival rate (DSR) for the 27-day incubation period. We identified four variables from the MRPP analyses of nest success as having potential to impact nest success. These variables included: grass height at the site level, visual obstruction at the site level, litter cover at the site level, and forb cover at the nest bowl. The variables were then combined with daily precipitation, daily minimum temperature, bird age, stage of incubation, and year. We did not model nest survival associated with nesting attempt because of a small number of renests ($n = 10$), although they were included in the analysis to test for seasonal variation. Daily weather variables were obtained from the nearest daily weather station located at Nisland, South Dakota, ~50 km from the center of the study area (South Dakota State Climate Office 2007). To reduce the effect of variable interaction in our models, variables that were correlated ($r > 0.70$) were not included in the same model.

TABLE 8.1

Mean vegetation characteristics of nest sites and random sites between years for Greater Sage-Grouse in northwestern South Dakota, 2006–2007.

	Nest			Random			Pooled		
Variable	2006 (n = 34)	2007 (n = 39)	$P \leq$	2006 (n = 35)	2007 (n = 39)	$P \leq$	Nest (n = 73)	Random (n = 74)	$P \leq$
Total cover (%)[1]	61.1 (2.3)	75.1(2.0)	0.01	55.8 (2.4)	66.1 (2.4)	0.01	68.6 (1.7)	61.2 (1.8)	0.01
Litter (%)	7.6 (0.8)	7.1 (0.6)	0.79	6.5 (0.7)	6.1 (0.4)	0.88	7.4 (0.5)	6.3 (0.4)	0.01
Grass cover (%)[1]	24.2 (1.9)	31.4 (1.8)	0.01	21.1 (1.9)	25.8 (2.0)	0.21	28.1 (1.4)	23.6 (1.4)	0.01
Max grass hgt. (cm)[2]	23.4 (0.9)	29.5 (1.6)	0.01	20.4 (0.8)	25.0 (1.1)	0.01	26.7 (1.0)	22.8 (0.7)	0.01
Max grass hgt. 0–5 m (cm)[2]	25.7 (0.9)	30.9 (2.0)	0.02	20.3 (0.8)	24.3 (1.1)	0.01	28.5 (1.2)	22.4 (0.8)	0.01
Visual obstruction (cm)	5.5 (0.6)	11.1 (1.0)	0.01	3.7 (0.4)	5.1 (0.6)	0.14	8.5 (0.7)	4.4 (0.4)	0.01
Visual obstruction 0 m (cm)[3]	20.8 (1.7)	29.4 (1.8)	0.01	10.5 (1.1)	8.9 (1.0)	0.13	25.4 (1.3)	9.6 (0.7)	0.01
Visual obstruction 1 m (cm)[3]	7.3 (0.9)	13.7 (1.7)	0.01	3.7 (0.5)	4.1 (0.6)	0.45	10.7 (1.0)	3.9 (0.4)	0.01
Sagebrush cover (%)	10.3 (0.8)	10.1 (0.8)	0.75	6.3 (0.8)	6.3 (0.7)	0.98	10.2 (0.6)	6.2 (0.5)	0.01
Sagebrush hgt. (cm)	25.8 (1.2)	29.7 (1.6)	0.04	23.8 (1.0)	24.0 (1.0)	0.97	27.9 (1.7)	23.9 (1.3)	0.01

NOTE: All values are reported as $\bar{x} \pm$ (SE). Variables with the same superscript number were correlated ($r > 0.70$) and not modeled together.

We used an information theoretic approach to evaluate support for models that influenced DSR (Burnham and Anderson 2002). We began by developing base models that included female age-classes, year, and constant survival. From these base models, we further explored the degree to which habitat and weather variables improved model fit. We used back-transformed estimates of DSR to estimate effects of variables on nest survival for the best supported models (Dinsmore et al. 2002). We then plotted DSR versus simulated values of variables to determine the effect of variables independently from one another. Estimated standard error for nest survival over the 27-day nesting cycle was calculated using the delta method (Seber 1982).

RESULTS

Nesting Parameters

We captured and attached transmitters to 53 female sage grouse (28 yearlings and 25 adults); 29 individuals were included both years for the resource selection analyses. Adults weighed (1,664 ± 14 g, $\bar{x}$ ± SE; $n = 43$) more than yearlings (1,524 ± 16, $n = 24$; $P < 0.01$). There were no differences in female mass between years ($P = 0.20$; $n = 67$). Nest initiation rate for all females was 98.0% and did not differ significantly between years ($P = 0.96$; $n = 67$) or with female age-class ($P = 0.92$; $n = 67$). Renest initiation rate was 25.8% (8/31) and did not differ significantly between years ($P = 0.19$; $n = 31$) or female age-class ($P = 0.62$; $n = 31$). Females were more likely to renest if their first nest was lost early in the incubation period ($P = 0.02$; $n = 31$). The number of nest observation days for first nests was 7.9 ± 1.3 SE days ($n = 8$) for females that renested and 14.6 ± 1.8 SE ($n = 23$) days for females that did not renest.

Average date of nest initiation for successful first nests was 24 April ± 1.6 SE ($n = 30$) days, with adults initiating egg laying approximately 6.7 days earlier than yearlings ($P = 0.02$; $n = 30$). Average hatch date for first nests was 31 May ± 1.5 SE ($n = 30$) days. Average date of renest initiation was approximately 15 days later (9 May ± 2.6 SE days; $n = 8$) than first nests, with hatch date occurring 14 June ± 2.0 SE days. Clutch size differed between nesting attempts (first nests: 8.3 ± 0.2 SE eggs; renests: 6.4 ± 0.6 SE; $P < 0.01$; $n = 64$), but not by nest fate ($P = 0.83$), female age-class ($P = 0.98$), or year ($P = 0.10$).

One adult female in 2007 nested approximately 30.3 km from lek of capture but most females nested close to leks. In 2006, successful nests were significantly closer to an active lek ($P = 0.04$; $n = 40$) than failed nests (1.5 ± 0.3 km vs. 2.9 ± 0.5 km, $\bar{x}$ ± SE); however, there was no difference in 2007 (2.5 ± 0.5 km vs. 3.2 ± 0.7 km, $P = 0.70$; $n = 39$), or when both years were combined (2.1 ± 0.3 km vs. 3.0 ± 0.4 km, $P = 0.13$; $n = 79$). The distance that adults and yearlings nested from the nearest active lek did not differ significantly (2.2 ± 0.3 km vs. 3.3 ± 0.5 km, $P = 0.08$; $n = 79$). Sixty-eight percent of nests were within 3 km of a documented active lek, and 97% of nests were within 7 km.

Average distance between an individual's nest in 2006 to its nest in 2007 was 1.08 ± 0.40 SE km ($n = 21$). There was no difference in nest site fidelity between adults and yearlings ($P = 0.65$; $n = 21$) or between nests that either failed or were successful the first year ($P = 0.47$; $n = 21$). Mean distance between failed first nests and subsequent renests was 1.85 ± 0.55 SE km ($n = 8$). Successful renests (0.95 ± 0.36 SE km) were not significantly closer to first nests than failed renests (2.03 ± 0.91 SE km, $P = 0.17$; $n = 8$).

Resource Selection

Distribution of total cover, grass cover, grass height, visual obstruction, and sagebrush height differed between nest sites in 2006 and 2007 ($P < 0.05$; Table 8.1). In addition, all screened vegetative characteristics differed between nests and random sites (Table 8.1). The minimum AIC_c model (AIC_c weight = 0.39; Table 8.2) of nest site selection included sagebrush canopy coverage at the site level ($\beta = 0.20$, SE = 0.06) and visual obstruction at the nest ($\beta = 0.22$, SE = 0.04; Table 8.2). Increasing sagebrush cover by 5% increased the odds of use approximately 6.1 times. Increasing visual obstruction at the nest by 2.54 cm increased the odds of use 3.2 times. Predictive ability of the top model (ROC values) was excellent at 0.93 and the Hosmer–Lemeshow goodness-of-fit test was nonsignificant ($P = 0.14$), indicating acceptable model fit.

A second model including sagebrush canopy coverage, visual obstruction at the nest, and average

TABLE 8.2

Selected models from logistic regression analysis (n = 39 models) predicting Greater Sage-Grouse nest sites (n = 73) versus random sites (n = 74) in northwestern South Dakota, 2006–2007.

Model[a]	Log(*L*)	*K*[b]	Δ AICc[c]	w_i[d]
Sagebrush cover + visual obstruction 0 m	−50.80	5	0.00	0.52
Sagebrush cover + visual obstruction 0 m + max grass hgt. 0–5 m	−49.82	6	0.22	0.47
Visual obstruction 0 m	−57.50	4	11.26	0.00
Sagebrush cover	−89.14	4	74.54	0.00
Intercept only	−101.89	2	95.85	0.00
Year	−101.89	3	97.92	0.00

[a] For ease of interpretation, year variable was excluded from model column. See Kaczor (2008) for full model set.
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC_c value.
[d] Model weight.

TABLE 8.3

Selected models for daily nest survival of Greater Sage-Grouse in northwestern South Dakota, 2006–2007.

Model[a]	*K*[b]	AIC_c	Δ AIC_c[c]	w_i[d]
Max grass hgt. + litter	3	225.79	0.00	0.23
Max grass hgt. + litter + daily precip. + precip. lag	5	226.75	0.96	0.15
Max grass hgt. + litter + daily precip.	4	227.37	1.60	0.11
Max grass hgt. + litter + bird age	4	227.77	1.98	0.09
Constant	1	252.71	26.92	0.00

[a] See Kaczor (2008) for full model set.
[b] Number of variables plus intercept.
[c] Change in AIC_c value.
[d] Model weight.

grass height within 5 m also had strong support (AIC_c weight = 0.35). Sagebrush canopy coverage and visual obstruction at the nest obtained the highest summed AIC_c weights of 0.99. The combined model of sagebrush canopy cover and visual obstruction at the nest had the greatest support, but there was less support for a single-factor model, although beta estimates for the two variables were similar ($\Delta\beta = 0.03$).

Nest Success

Most nests were located under Wyoming big sagebrush (90%) or silver sagebrush (7%; $n = 79$). One nest was against a large boulder, and another was in a dense stand of prairie cordgrass (*Spartina pectinata*). Egg hatchability averaged 78.3 ± 2.1 SE % ($n = 513$). Constant nest survival rates with no covariates were 45.6 ± 5.3 SE %, but that was a poor model of DSR. The best model for DSR (AIC_c weight = 0.23) included grass height and litter cover (Table 8.3). Three other models were $\Delta AIC_c \leq 2$ units of the top model. Grass height had a positive association with DSR ($\beta = 0.15$, SE = 0.03; Fig. 8.2), whereas percent litter cover had a negative association on DSR ($\beta = -0.08$, SE = 0.03); both factors were present in all of models with $\Delta AIC_c < 2.0$.

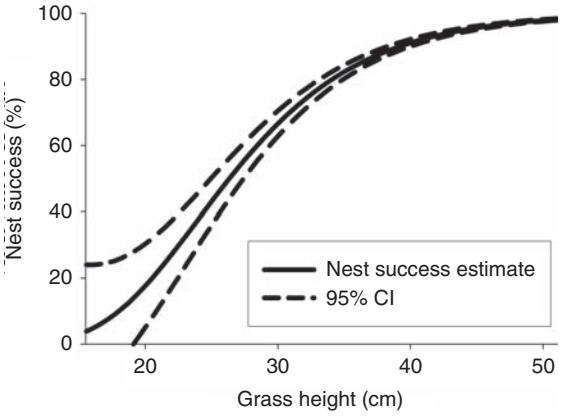


Figure 8.2. Effect of grass height on nest success of Greater Sage-Grouse in northwestern South Dakota, 2006–2007. Nest success estimates were derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

The second-ranked model (AIC_c weight = 0.15) included grass height, litter, daily precipitation, and a 1-day lag of precipitation. Daily precipitation had a positive association with DSR (β = 29.5, SE = 40.4) and the 1-day lag of precipitation was negatively associated with DSR (β = –1.89, SE = 0.77). These variables were only included in supported models when combined with grass height and litter. The third- and fourth-ranked models both included grass height and litter along with the variables daily precipitation and bird age, respectively. Nest success differed between years from 37.7 ± 7.3 SE % in 2006 to 52.5 ± 7.2 SE % in 2007. However, adding a year effect to the top model did not improve model fit.

DISCUSSION

Our study of Greater Sage-Grouse on the easternmost portion of their range in South Dakota identified interesting aspects of sage grouse ecology that have not previously been documented. Female body condition was above average and nesting initiation rates were also high. Similar to other studies, sagebrush cover was an important variable in nest site selection, but at a much lower density than expected. Grass structure, which far exceeded range-wide estimates, played an important role in providing increased cover for successful nests (Connelly et al. 2004). Overall, nest success was within range-wide estimates, suggesting certain features of the habitat condition in South Dakota are productive for sage grouse.

Nesting Parameters

Nest initiation rates for sage grouse are generally low compared to other prairie grouse (Bergerud 1988). However, estimates of nesting initiation based on telemetry are probably underestimated in the literature, as follicular development indicated that at least 98.2% of females laid eggs the previous spring in Idaho (Dalke et al. 1963, Schroeder et al. 1999). Nonetheless, nest initiation rates were high in this study relative to range-wide estimates (Connelly et al. 2004). Females in our study were approximately 63 g (~4%) heavier than the average for 673 individuals in eight other studies (Schroeder et al. 1999). Heavier body mass in female Wild Turkeys (*Meleagris gallopavo*) increased the likelihood of breeding (Porter et al. 1983, Hoffman et al. 1996). Sage grouse exhibit considerable temporal variation in nest initiation rates between years, which may be related to nutrition before and during the breeding season (Hungerford 1964, Barnett and Crawford 1994, Moynahan et al. 2007). High rates of initiation suggest that habitat conditions in our study site were above average.

Renesting rates in sage grouse are highly variable (0–87%), and are linked to environmental effects and habitat quality (Schroeder 1997, Moynahan et al. 2007). Low renesting rates may be related to low primary productivity in the arid and semiarid environments occupied by sage grouse (Schroeder and Robb 2003). For example, Moynahan et al. (2007) found no renesting by sage grouse in dry years with little vegetative growth. In North Dakota, Herman-Brunson et al. (2009) reported 9.5% renesting in sage grouse. The relatively high proportion of renesting females in our study and greater female mass suggest that nesting habitat in South Dakota is of higher quality than elsewhere in sage grouse range. The inverse relationship between length of incubation and renesting propensity suggests that the condition of the female may decline as

incubation progresses. An inverse relationship between the duration of incubation and renesting has also been shown elsewhere (Aldridge and Brigham 2001, Herman-Brunson 2009, Martin et al., this volume, chapter 17).

Nest Success

Sage grouse in South Dakota selected nest sites with higher sagebrush cover and placed their nests beneath sagebrush plants with greater horizontal cover (VOR) than random sites. Shrub density (correlated with sagebrush cover) and nest-bowl VOR were important predictors of sage grouse nest sites in North Dakota (Herman-Brunson et al. 2009). Connelly et al. (2000) recommended 15–25% sagebrush canopy coverage for nesting sage grouse, and this recommendation has been confirmed with a range-wide meta-analysis (Hagen et al. 2007). In South Dakota, nesting sage grouse selected for sagebrush with the highest densities and protective cover, but that was less than recommended values. In contrast to sagebrush, grass structure in South Dakota exceeds both management recommendations and range-wide averages (Connelly et al. 2000, Hagen et al. 2007). Western South Dakota forms a transition zone between the northern wheatgrass–needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). Thus, while South Dakota had less than expected sagebrush cover for sage grouse, the grass structure likely compensated for the low sagebrush densities in providing cover for nests. Grass structure is highly correlated with annual precipitation; therefore, periodic drought may reduce nest cover for sage grouse. Poor grazing management in areas with low sagebrush cover could reduce grass structure, which may have detrimental effects on sage grouse nesting.

Sage grouse nest success varies widely across the range, from 14.5% (Gregg 1991) to 70.6% (Chi 2004), and is generally believed to be related to habitat conditions (Connelly et al. 1991, Aldridge and Brigham 2002, Hagen et al. 2007). Our estimate of nest success was similar to that of other sage grouse studies (48%; Connelly et al. 2004), despite the fact that available sagebrush canopy coverage was less than other areas. Successful nests in our study had taller grass structures than failed nests. Thus, tall grass differentiated not only suitable nest sites, but also nesting success. Nesting cover also increased nest success in Alberta, and was suggested to provide ample nest concealment in both sagebrush and non-sagebrush overstories in Washington (Sveum et al. 1998, Aldridge and Brigham 2002). Although litter cover entered our models as being an important predictive variable for nest success, the impact litter actually has on nest success is unknown. Litter may be greater after productive growing seasons, or be lower after intensive grazing pressure (Hart et al. 1988, Naeth et al. 1991).

Our results suggest that some aspects of sage grouse habitat in our study area were conducive to maintaining sage grouse populations despite being outside of current management recommendations (Connelly et al. 2000). Although management recommendations were based on existing knowledge, our habitat also provided the necessary requirements for the nesting period, which may be an important consideration for land managers elsewhere in sage grouse ranges.

Management Implications

If sage grouse populations continue to decrease or remain listed as a sensitive species, sagebrush conservation and enhancement could be a top priority for land management agencies to enable sage grouse persistence in western South Dakota. Management for greater grass and sagebrush cover and height, and reduced conversion to tillage agriculture, could be encouraged to protect remaining habitats. Grazing by domestic sheep (*Ovis aries*) can reduce sagebrush cover (Baker et al. 1976), thereby reducing habitat quality for sage grouse. Domestic sheep grazing is not widespread in South Dakota, but was common on both private and public lands in our study area.

Range management practices that could increase sagebrush and grass cover and height include: rest-rotation grazing, where the rested pasture is not grazed until early July to allow for undisturbed nesting, or reduced grazing intensities or seasons of use to reduce impacts on sagebrush and grass growth (Adams et al. 2004). Land managers could develop grazing plans that leave or maintain grass heights $\geq$26 cm to try to maintain 50% nest success. In addition, we suggest annual grazing utilization not exceed 35% in order to improve rangeland conditions, particularly sagebrush cover (Holechek et al. 1999).

Wyoming big sagebrush typically recovers from a fire in 50–120 years (Baker 2006), and because of the restricted distribution and limited cover of sagebrush in South Dakota, we suggest limited use of prescribed fire or herbicides in areas with sagebrush.

ACKNOWLEDGMENTS

Funding for this study was provided by the Bureau of Land Management (ESA000013), U.S. Forest Service Rocky Mountain Research Station (05-JV-11221609-127), U.S. Forest Service Dakota Prairie National Grasslands (05-CS-11011800-022), and support from South Dakota State University. Field assistance was provided by C. Berdan, T. Berdan, B. Eastman, B. Hauser, T. Juntti, J. Nathan, S. Harrelson, and T. Zachmeier. A number of volunteers assisted during capture and radio-collaring of females and chicks. A. Apa assisted with training on trapping techniques. We also acknowledge and appreciate those land owners who granted us permission to conduct this study on their private lands. We thank D. Turner, J. Sedinger, and an anonymous reviewer for their comments on prior versions of this manuscript. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

Adams, B. W., J. Carlson, D. Milner, T. Hood, B. Cairns, and P. Herzog. 2004. Beneficial grazing management practices for sage-grouse (*Centrocercus urophasianus*) and ecology of silver sagebrush (*Artemisia cana*) in southeastern Alberta. Technical Report, Public Lands and Forests Division, Alberta Sustainable Resource Development. Pub. No. T/049.

Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537–543.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood-rearing habitat use in southern Canada. Journal of Wildlife Management 66: 433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions 14:983–994.

Baker, M. F., R. L. Eng, J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on the effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–170.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114–118.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pp. 578–685 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. Wildlife Management Institute, Minneapolis, MN.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools> (10 January 2006).

Booth, D. T., S. E. Cox, T. W. Meikle, and C. Fitzgerald. 2006. The accuracy of ground-cover measurements. Rangeland Ecology and Management 59:179–188.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139–156.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Chi, R. Y. 2004. Greater Sage-Grouse on Parker Mountain, Utah. M.S. thesis, Utah State University, Logan, UT.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage-grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521–524.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846–849.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811–841.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–64.

Dinsmore, S. J., and D. H. Johnson. 2005. Population analysis in wildlife biology. Pp. 154–184 *in* C. E. Braun (editor), Techniques for wildlife investigations and management. 6th ed. The Wildlife Society, Bethesda, MD.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Floyd, D. A., and Anderson, J. E. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221–228.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage-grouse in Oregon. M.S. thesis, Oregon State University, Corvallis, OR.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of Greater Sage-Grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(Supplement): 42–50.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282–286.

Herman-Brunson, K. H., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of Greater Sage-Grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology 15:237–246.

Hoffman, R. W., M. P. Luttrell, and W. R. Davidson. 1996. Reproductive performance of Merriam's Wild Turkeys with suspected *Mycoplasma* infection. Proceedings of National Wild Turkey Symposium 7:145–151.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. Rangelands 21:12–16.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. John Wiley and Sons Inc., New York, NY.

Hungerford, C. R. 1964. Vitamin A and productivity in Gambel's Quail. Journal of Wildlife Management 28:141–147.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota and the northern Great Plains. South Dakota State University. Brookings, SD.

Johnson, P. R. 1976. Soil survey of Butte County, South Dakota. U.S. Department of Agriculture, South Dakota Agricultural Experiment Station, Brookings, SD.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings, SD.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late: conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Mielke, P. W., and K. J. Berry. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York, NY.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater Sage-Grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Naeth, M. A., A. W. Bailey, D. J. Pluth, D. S. Chanasyk, and R. T. Hardon. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems in Alberta. Journal of Range Management 44:7–12.

Pollard, J. H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27:991–1002.

Porter, W. F., G. C. Nelson, and K. Mattson. 1983. Effects of winter conditions on reproduction in a northern Wild Turkey population. Journal of Wildlife Management 47:281–290.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–298.

SAS Institute Inc. 2007. JMP version 7. Cary, NC.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933–941.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). A. Poole and F. Gill, (editors), The Birds of North America No. 425. The Birds of North America, Inc., Philadelphia, PA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin and Company Ltd., London.

South Dakota Department of Game, Fish, and Parks. 2006. South Dakota comprehensive wildlife conservation plan. South Dakota Department of Game, Fish, and Parks, Wildlife Division Report 2006-08, Pierre, SD.

South Dakota State Climate Office. 2007. Office of the State Climatologist. <http://climate.sdstate.edu> (15 December 2007).

Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. M. Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4–12.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265–269.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

PLOS | ONE

RESEARCH ARTICLE

Microhabitat Conditions in Wyoming's Sage-Grouse Core Areas: Effects on Nest Site Selection and Success

Jonathan B. Dinkins[1☯]*, Kurt T. Smith[1☯], Jeffrey L. Beck[1], Christopher P. Kirol[1], Aaron C. Pratt[1], Michael R. Conover[2]

1 Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming, United States of America, **2** Department of Wildland Resources, Utah State University, Logan, Utah, United States of America

☯ These authors contributed equally to this work.
* jdinkins@uwyo.edu

CrossMark
click for updates

OPEN ACCESS

Citation: Dinkins JB, Smith KT, Beck JL, Kirol CP, Pratt AC, Conover MR (2016) Microhabitat Conditions in Wyoming's Sage-Grouse Core Areas: Effects on Nest Site Selection and Success. PLoS ONE 11(3): e0150798. doi:10.1371/journal.pone.0150798

Editor: R. Mark Brigham, University of Regina, CANADA

Received: October 26, 2015

Accepted: February 20, 2016

Published: March 22, 2016

Copyright: © 2016 Dinkins et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: Research funding was provided by: American Colloid Company; Anadarko Petroleum Corporation; Bates Hole, Bighorn Basin, South-Central, Southwest, and Wind River/Sweetwater River Local Sage-Grouse Working Groups; Jack H. Berryman Institute; Lincoln County Predator Management Board; Margaret and Sam Kelly Ornithological Research Fund; Predatory Animal District of Sweetwater County; School of Energy Resources and Wyoming Reclamation and

Abstract

The purpose of our study was to identify microhabitat characteristics of greater sage-grouse (*Centrocercus urophasianus*) nest site selection and survival to determine the quality of sage-grouse habitat in 5 regions of central and southwest Wyoming associated with Wyoming's Core Area Policy. Wyoming's Core Area Policy was enacted in 2008 to reduce human disturbance near the greatest densities of sage-grouse. Our analyses aimed to assess sage-grouse nest selection and success at multiple micro-spatial scales. We obtained microhabitat data from 928 sage-grouse nest locations and 819 random microhabitat locations from 2008–2014. Nest success was estimated from 924 nests with survival data. Sage-grouse selected nests with greater sagebrush cover and height, visual obstruction, and number of small gaps between shrubs (gap size $\geq$0.5 m and <1.0 m), while selecting for less bare ground and rock. With the exception of more small gaps between shrubs, we did not find any differences in availability of these microhabitat characteristics between locations within and outside of Core Areas. In addition, we found little supporting evidence that sage-grouse were selecting different nest sites in Core Areas relative to areas outside of Core. The Kaplan-Meier nest success estimate for a 27-day incubation period was 42.0% (95% CI: 38.4–45.9%). Risk of nest failure was negatively associated with greater rock and more medium-sized gaps between shrubs (gap size $\geq$2.0 m and <3.0 m). Within our study areas, Wyoming's Core Areas did not have differing microhabitat quality compared to outside of Core Areas. The close proximity of our locations within and outside of Core Areas likely explained our lack of finding differences in microhabitat quality among locations within these landscapes. However, the Core Area Policy is most likely to conserve high quality habitat at larger spatial scales, which over decades may have cascading effects on microhabitat quality available between areas within and outside of Core Areas.

Restoration Center at the University of Wyoming; Uinta County Predator Management Board; Utah Agricultural Experiment Station; Wyoming Animal Damage Management Board; Wyoming Sage-grouse Conservation Fund of the Wyoming Game and Fish Department; Wyoming Wildlife and Natural Resource Trust. Funding for analysis and publication of this paper was provided by the State of Wyoming Legislature through the Wyoming Wildlife and Natural Resource Trust on behalf of the Wyoming Sage-Grouse Implementation Team. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Quantity and quality of breeding habitat have been suggested as the most important factors dictating the productivity of greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations [1,2,3]. Studies have reported that sage-grouse select nest sites based on a preference for different microhabitat characteristics, such as sagebrush density [4,5], sagebrush cover [6,7], shrub height [8], grass height [7,8,9], and grass cover [7,10]. These studies all indicated that sage-grouse choose nest locations in habitats with greater concealment cover. However, there are differences in the quality of local microhabitat available as nesting habitat for female sage-grouse across Wyoming.

While sage-grouse select for microhabitat characteristics that provide greater concealment cover from predators and protection from weather, selection of habitat is limited to the range of microhabitat conditions that are available. Microhabitat characteristics around a nest, such as sagebrush cover and grass height, can facilitate or impede a predator from depredating a nest [11,12], and this varies among different types of nest predators [11,13]. Sage-grouse consistently select for greater sagebrush cover [7,9,14,15,16]; however, the connection between sagebrush cover and nest success has been more variable with many studies failing to find a relationship between nest success and sagebrush cover with some exceptions [8,17,18]. The current knowledge of sage-grouse nesting ecology indicates that sagebrush (or shrub) cover is important, but the effect of sagebrush cover on nest success among local areas is variable. Holloran et al. [9] suggested that within patch scales, sagebrush metrics remain relatively constant throughout and among breeding seasons, whereas, grass cover and height were more variable and dependent on weather conditions. A study in southeast Montana and northeast Wyoming found that grass height variability influenced by spring precipitation was highly predictive of nest success in sage-grouse [19]. Habitat quality is highly variable and depends on multiple environmental and anthropogenic factors. Variability in the condition of available microhabitat throughout sage-grouse range may significantly influence specific life-history stages and associated vital rates (e.g., nest success). Therefore, studies across broader ranges and more diverse microhabitat have the greatest potential to identify microhabitat variables that influence nest selection and success of sage-grouse at regional scales.

As a result of the 2008 Wyoming Governor's Sage-grouse Executive Order, the State of Wyoming implemented the Core Area Policy to conserve sage-grouse populations in Wyoming [20]. This policy focuses on minimizing impacts to the highest quality sage-grouse habitats [21,22]. We have compiled an expansive dataset designed to evaluate sage-grouse nest site selection and nest success, where data were collected from multiple regions throughout Wyoming starting in the initial year of the Core Area Policy. The purpose of our study was to use microhabitat data collected over a broad range of sagebrush habitats in Wyoming to 1) identify microhabitat characteristics that influence sage-grouse selection of nest sites, 2) compare available microhabitat within and outside of Core Areas, 3) compare microhabitat used by sage-grouse for nesting between areas protected and not protected under the Core Area Policy, and 4) evaluate the influence of microhabitat on nest success and compare nest success within and outside of Core Areas. Our analysis contains an evaluation of several Core and non-Core Areas and distinct sage-grouse populations within Wyoming.

Study Areas

Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations and mountain big sagebrush (*A. t. vaseyana*) at higher elevations dominated our study areas [23]. Black sagebrush (*A. nova*) and/or low sagebrush (*A. arbuscula*) were found on exposed ridges. Other shrub species common to various study areas included alderleaf mountain mahogany

(*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*.), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at higher elevations. Data within our study areas were collected 2008–2014, but active data collection differed for some of the study areas (Table 1). Annual precipitation within study areas ranged from approximately 22.3 cm to 49.3 cm (mean = 32.5 cm [2.7 SE]). All study areas had some anthropogenic features. In the less disturbed study areas this mainly consisted of unimproved 4-wheel drive roads. Oil and gas extraction activities occurred in each of the study areas (range 0.004–0.236 wells per km^2) and consisted of conventional natural gas, coalbed methane natural gas, and/or conventional oil with an average of 0.18 per km^2 outside Core Areas and 0.01per km^2 within Core Areas. Livestock grazing by domestic sheep and cattle was a primary land use in all of the study areas.

Atlantic Rim

The Atlantic Rim study area was located in southern Carbon County, Wyoming, extending approximately 77 km north and south between Rawlins and Baggs (Fig 1). This study area was located within and adjacent to the South Rawlins and Greater South Pass Core Areas. The area included approximately 64% federal, 5% state, and 31% private lands. The Atlantic Rim is within the semi-desert grass-shrub zone and is characterized by sagebrush steppe with low average annual precipitation. Elevation within the study area ranged from 1,982 to 2,529 m. Major land uses included oil and gas extraction.

Bighorn Basin

The Bighorn Basin study area was located in Big Horn and Washakie counties, Wyoming (Fig 1). This study area was located within and adjacent to the Hyattville, Shell, and Washakie Core Areas. The area extends northeast of Greybull, Wyoming and south to near Ten Sleep, Wyoming in the eastern Bighorn Basin on the west slope of the Bighorn Mountains. The area included approximately 74% federal, 7% state, and 19% private lands. Elevation within the study area ranged from 1,300 to 2,850 m. Major land uses in this area included bentonite mining.

Jeffrey City

The Jeffrey City study area was in portions of Fremont and Natrona counties, Wyoming (Fig 1). This study area was located within and adjacent to the Greater South Pass Core Area. The area included approximately 81% Federal, 7% State, and 12% privately administered lands. Elevation ranged from 1,642 to 2,499 m. There is interest to resume uranium mining, which historically was once a major land use in the area.

Table 1. Summary of nest and random location sample sizes used for occurrence, availability (random-random), and nest success analyses, in central and southwestern Wyoming, USA, 2008–2014.

Sage-grouse study area	Years	Nests	Random
Atlantic Rim	2008–2011	123	122
Bighorn Basin	2011–2014	291	290
Jeffrey City	2011–2014	270	166
Southwest Wyoming	2008–2011	193	190
Stewart Creek	2008–2011	51	51
Total of all studies	2008–2014	928	819

doi:10.1371/journal.pone.0150798.t001

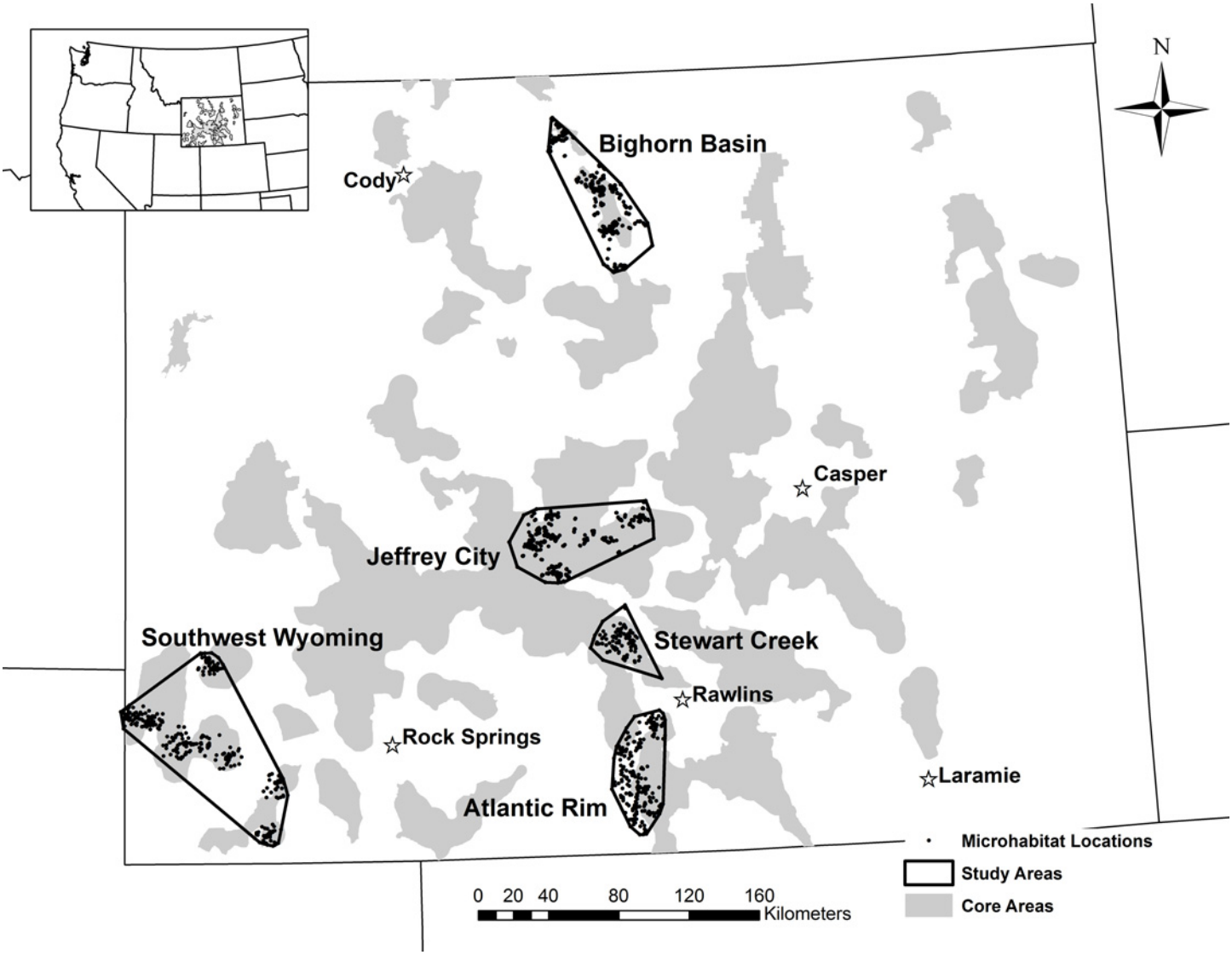


Fig 1. Map of study areas and microhabitat sampling points across five regions in central and southwestern Wyoming, USA, 2008–2014. Boundaries for each study area were demarcated by a 100% minimum convex polygon encompassing 928 sage-grouse nests and 819 random locations. However, the southwest Wyoming minimum convex polygon was an aggregation of 8 separate 8-km areas around sage-grouse leks. Locations of 31 sage-grouse Core Areas are also illustrated in gray.

doi:10.1371/journal.pone.0150798.g001

Southwest Wyoming

The Southwest Wyoming study area consisted of eight distinct study sites that were approximately 16 km in diameter centered on leks; this distance was based on results found by Holloran and Anderson [24] that indicated 93% of 415 nests were within 8.5 km from leks in central and southwestern Wyoming (Fig 1). The Southwestern Wyoming study area was located within and adjacent to the Fontenelle, Sage, and Uinta Core Areas. Five study sites were located in Lincoln, one in Sweetwater, and two in Uinta counties, Wyoming. Study sites were chosen to provide a representation of overall sage-grouse nesting habitat in southwestern Wyoming. Elevation ranged from 1,925 to 2,550 m. The area included approximately 65% Federal, 4% State, and 31% privately administered lands. Oil and gas development was present in 37.5% of the study area.

Stewart Creek

The Stewart Creek study area was located in northern Carbon County, approximately 32.2 to 64.4 km north and west of Rawlins, Wyoming (Fig 1). This study area was located within and adjacent to the Greater South Pass Core Area. The area includes approximately 70% federal, 5% state, and 25% privately administered lands. The Stewart Creek area is within the semi-desert grass-shrub zone, characterized by sagebrush steppe with low annual precipitation. Elevation ranged from 1,982 to 2,529 m.

Methods

Capture and monitoring

We captured and radio-marked female sage-grouse from leks in spring by spot-light and hoop-net methods [25,26] from 2008–2014. We also used roosting locations of radio-marked adult females captured in spring to capture and radio-mark additional females in late summer each year. We aged females as juveniles or adults based on the shape and condition of the outermost wing primaries, the outline of the primary tail feathers, and coloration of undertail coverts [27,28]. We attached radio transmitters (22 g, Model A4060; Advanced Telemetry Systems Incorporated, Isanti, MN, USA) to females with a PVC-covered wire necklace. In the Bighorn Basin and Jeffrey City study areas, we attached GPS transmitters (22-g Solar Argos/GPS PTT-100, Microwave Telemetry, Columbia, MD, USA or Model 22 GPS PTT, North Star Science and Technology, King George, VA, USA) via rump mounts instead of necklace radio collars to a small portion of captured females. These GPS transmitters were programmed to acquire 4 locations per day via satellite (Argos, www.argos-system.org) from 15 March to 30 April, and 5 locations per day from 1 May to 24 August. We located VHF-collared females weekly beginning mid-to-late April each year with R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA, USA). All sage-grouse were captured, marked, processed, and monitored in adherence with approved protocols (Atlantic Rim and Stewart Creek studies [Wyoming Game and Fish Department {WGFD} Chapter 33 permits 572 and 699 and University of Wyoming Institutional Animal Care and Use Committee {UW IACUC} protocol 03032009]; Bighorn Basin study [WGFD Chapter 33–800 permit and UW IACUC protocols 03142011 and 20140228JB00065]; Jeffrey City study [WGFD Chapter 33–801 permit and UW IACUC protocols 03132011 and 20140128JB0059]; Southwest Wyoming study [WGFD Chapter 33 permit 657 and Utah State University IACUC protocol 1357]).

We located nests by circling a radio-marked (necklace collars) female until the surveyor visually located the female under a shrub or isolated the hen's location. To minimize human-induced nest depredation or nest abandonment, we subsequently monitored nests of radio-marked females with triangulation from a distance of at least 30 m. For GPS-equipped females, we visually inspected potential nests after the female left a location of clustered GPS points. Nest success (i.e., nests with at least 1 hatched egg) was determined by examining egg shells after the female was no longer located at the nest site.

Microhabitat sampling

We sampled microhabitat at nest and random locations for all study areas in all years with the exception that no random sampling was conducted in Jeffrey City during 2014. In the Atlantic Rim, Southwest, and Stewart Creek study areas, random locations for comparison to nest locations were established throughout the study area within 8 km of all leks where sage-grouse capture was conducted with ArcMap. We used Northwest GAP land-cover data [29] to constrain random locations to sagebrush habitats while excluding areas of inappropriate habitat such as

exposed rock, open water, and conifer stands. In the Bighorn Basin and Jeffrey City study areas, we constrained random sampling at a random distance and direction 0.1–0.5 km from each paired nest location [30]. We chose a simulated nest site at random locations by selecting the closest shrub taller than or equal to 30 cm [9,31].

We used established protocols to measure the vegetation characteristics of microhabitat surrounding nests and random locations [5]. We began sampling nest microhabitat plots after the first successful hatch and attempted to sample nest and random locations concurrently within 2 weeks of known nest fate. We measured microhabitat characteristics along two perpendicular 10-m transect lines centered on each nest or random location extending in each cardinal direction (Table 2). We recorded shrub canopy cover with the line intercept method [32,33]. We

Table 2. Descriptions of microhabitat variables used to evaluate selection, availability (random-random), and nest success of sage-grouse. Data were collected at 928 sage-grouse nests and 819 random locations in in 5 study areas in Wyoming, USA, 2008–2014.

Variable Name	Description
Categorical Variables	
Nest Shrub Spp.	Shrub species at nest or center of random plots. Classified as sagebrush or non-sagebrush
Shrub Characteristics	
Shrub[1,2]	Mean total shrub cover (%)
Artr[1,2]	Mean big sagebrush cover (%)
Shrub_H	Mean shrub height (cm)
Artr_H	Mean big sagebrush height (cm)
Gap[3]	Count of spaces between shrubs
VO	Mean visual obstruction (horizontal; cm) 5 m from plot location
Grass Height	
PerGrass_H	Mean maximum perennial droop height (cm)
ResGrass_H	Mean maximum residual droop height (cm)
Herbaceous Canopy Cover (%)[4]	
AnGrass[4,5]	Mean annual grass cover
PerGrass[4,5]	Mean perennial grass cover
ResGrass[4,5]	Mean residual grass cover
FoodF[4,6]	Mean food forb cover
NFoodF[4,6]	Mean non-food forb cover
Ground Cover (%)[4]	
BGround[4,7]	Mean bare cover
Cactus[4]	Mean cactus cover
BioCrust[4]	Mean biological soil crust cover
Rock[4,7]	Mean gravel and rock cover
Litter[4]	Mean litter cover

[1]Cover assessed at 1, 2.5, and 5 m away from transect center

[2]Proportion of Artr to Shrub assessed at 1, 2.5, and 5 m away from transect center [3]Gap spacing was categorized as ≥0.5 m and <1.0 m ($Gap_{0.5m}$), ≥1 m and < 2.0 m (Gap_{1m}), ≥2.0 m and <3.0 m (Gap_{2m}), and ≥3.0 m and <4.0 m (Gap_{3m}) counted along transect lines

[4]Cover assessed at 1.5 and 3.5 m away from transect center and between 2.5–3.5 m away from transect center

[5]Variables combined to assess total grass cover (Grass)

[6]Variables combined to assess total forb cover (Forb)

[7]Variables combined to assess total bare, gravel and rock ground cover (BareRock)

doi:10.1371/journal.pone.0150798.t002

measured height (cm) at each shrub that intercepted the line. Average canopy cover and height were quantified as total shrub and big sagebrush species. Sagebrush cover and height calculations excluded mat-forming sub-shrub species (e.g., prairie sagewort [*A. frigida*]) that could not be considered concealment cover for nests. Average sagebrush and shrub cover were calculated at three microhabitat spatial scales by averaging values from the two perpendicular lines from the nest or random location to 1, 2.5, or 5 m away from the nest or random location. We estimated visual obstruction to the nearest 5 cm by visually estimating the closest point to the ground visible on a modified Robel pole from 5 m away from nest and random locations and 1-m above the ground [34,35]. We estimated cover of annual grasses, perennial grasses, residual perennial grasses, food forb cover (for list, *see* [7]), non-food forb cover, gravel and rock, bare soil, biological soil crust, and litter by recording cover in 6 cover classes within 20 x 50 cm quadrats (0.1 m^2; [36]). Quadrats were placed along each transect line at the center of each transect (nest bowl or center of random location) and centered at 1 and 3 m from the transect intersection in each cardinal direction for a total of $n = 9$ quadrats at each microhabitat plot. Cover classes were demarcated as 1 = 0.1–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. Average cover for quadrat variables were calculated at three microhabitat spatial scales by averaging values from the inner 5 quadrats (transect center and quadrats place 1 m from the transect center; 1 m spatial scale), the outermost 4 quadrats (values describing average values 2.5 to 3.5 m [width of the quadrat frame] away from the nest or random location), and all 9 quadrats (3.5 m spatial scale). We measured the height of perennial and residual perennial grasses (cm) as the tallest portion of the plant (droop height) within 1 m of each quadrat.

Descriptions of shrub characteristics (sagebrush and total shrub cover, sagebrush and total shrub height, gaps in shrub cover, and visual obstruction), grass height (perennial and residual grass height), herbaceous canopy cover (annual, perennial, residual grass, and forb cover), and ground cover (bare ground, biological soil crust, rock, and litter cover) variables calculated from transect lines, Robel poles, and quadrats are provided in Table 2. In addition to measured shrub characteristics, we calculated the proportion of sagebrush to total shrub cover (ARTRpShr) at all microhabitat spatial scales, and we generated number of shrub cover gaps in four categories. Shrub cover gaps were classified as $Gap_{0.5m}$ ($\geq$0.5 m and $<$1.0 m), Gap_{1m} ($\geq$1 m and $<$ 2.0 m), Gap_{2m} ($\geq$2.0 m and $<$3.0 m), or Gap_{3m} ($\geq$3.0 m and $<$4.0 m), then the number of each gap classification was summed along transect lines. The proportion of sagebrush to total shrub within plots was intended to assess differences in shrub composition relative to sagebrush as a measure of shrub diversity between sage-grouse nests and random locations, within and outside of Core Areas for random and nest locations, and nest success. We also recorded the dominant shrub species at the center of nest and random locations, which was used as a categorical variable classifying the shrub directly above a nest or center of a random location as sagebrush or non-sagebrush.

Data analysis

For all analysis types, we used an information theoretic approach for modeling [37]. All statistical analyses were conducted in R [38]. We compared models with Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights w_i; [39] with function 'model.sel' in package MuMIn version 1.13.4 in R. We screened each variable to identify potentially informative variables, which were defined as variables with regression coefficient values with 85% confidence intervals (CIs) that did not overlap zero [40]. For variable screening, variables with 85% CIs that overlapped zero were eliminated from all further AIC_c modeling. We based our inference on regression models within 4 AIC_c of the top selected model [39]. For variables

measured at multiple microhabitat spatial scales, we compared single variable models and only used the microhabitat spatial scales that were not correlated or the variable with the lowest AIC_c in additive models. Our modeling approach allowed us to use variables with the most predictive potential to make inferences about selection and nest success [41] at different microhabitat scales. Model averaging of coefficients and standard errors was employed when there was model uncertainty, which was defined as multiple competing models within 4 ΔAIC_c of the top model. For all competitive final models, we report 95% CI for parameter estimates and odds ratios, because we considered predictor variables with 95% CI not overlapping zero to be precise and predictor variables that had 95% CI that overlapped zero to be marginal. Thus, we focused our interpretations on the precise predictor variables.

All models included year (2008–2014) and the 30-year normal of annual precipitation as random effects to account for seasonal weather and overall habitat differences among nest and/or random locations across years and study areas. The 30-year normal of annual precipitation consistently accounted for more variation among sampling locations than study area; thus, we used the 30-year normal of precipitation as a random factor rather than study area. The 30-year normal of annual precipitation was extracted at a 1-km spatial resolution from PRISM [42]. Differences in sampling design for random locations were also accounted for with these random effects. To prevent multicollinearity, we did not include any two co-varying variables ($|r \geq 0.65|$) in any model as determined by a Pearson's correlation matrix. When variables were correlated, we included the variable with the lowest AIC_c in that model.

Selection and availability models. We used binomial generalized mixed models (GLMMs) to evaluate 1) nest selection of sage-grouse, 2) availability of microhabitat within and outside of Core Areas, and 3) to compare nest selection by sage-grouse within and outside of Core Areas. For ease of interpretability, we referred to these analysis types as 1) nest-random, 2) random-random, and 3) nest-nest. The nest-random analysis employed a use-availability design to evaluate sage-grouse nest site selection with binary logistic regression [43], whereas, the random-random and nest-nest analyses were intended to classify differences in microhabitat between locations (random or nest) within and outside of Core Areas.

We fitted GLMMs with year and 30-year normal of precipitation as random effects with function 'lmer' in package lme4 version 1.1–7 in R. Random locations were coded as the reference category for our nest-random analysis, random locations outside of Core Areas were coded as the reference category for our random-random analysis, and nest locations outside of Core Areas were coded as the reference category for our nest-nest analysis. Microhabitat variables considered as predictors included shrub characteristics, grass height, herbaceous canopy cover, and ground cover variables (Table 2). We compared all possible combinations of informative variables as additive models for each analysis type with AIC_c and w_i. The interpretations of change in odds ratios (selection probabilities) per unit change in variables were calculated as the median change in odds bound by the range of variable values for that variable with the other variables in the model held at their mean value. We report means and SE for nest-random microhabitat data in S1 Table.

Nest success models. Nest success was evaluated with a mixed effects version of the Cox proportional hazard (Cox PH) model using function 'coxme' in package coxme version 2.2–4 in R. We used Cox PH to identify relationships between microhabitat predictor variables and nest success. Analysis of nest success was based on time-to-event data, and Cox PH models are commonly used to analyze time-to-event survival data [44]. The risk of failure (hazard ratio) is a function of the non-parametric baseline hazard, and the parametric predictor variables affecting failure [45]. Thus, beta estimates were presented as the risk of a nest failing with positive beta values indicating a variable was positively related to a greater risk of nest failure. In Cox PH models, the baseline hazard is assumed to have a proportional hazard of failure over time

(proportional hazard assumption) for all predictor variables [45]. Thus, we tested the proportional hazard assumption for each predictor variable with the function 'cox.ph' in the coxme package in R [46]. As in our GLMMs, we fit Cox PH models with year and 30-year normal of precipitation as random effects.

We assessed the effect of microhabitat including shrub characteristics, grass height, herbaceous canopy cover, and ground cover variables on nest success (Table 2). In addition to the microhabitat variables, we compared nest success within and outside of Core Areas with a categorical variable (Cor_NonCore). All possible combinations of informative variables were included as additive models and compared with AIC_c and w_i. Nest success estimates were calculated with the Kaplan-Meier product-limit estimator [47].

Results

We obtained microhabitat samples at 928 nests and 819 random locations across study areas from 2008 to 2014 (Table 1). All nests and random locations (n = 1,747) were used in the nest-random analysis, 819 random locations were used in the random-random analysis, and 928 nests were used in the nest-nest analysis. We recorded information on nest success at 924 nests, which were used in nest success analysis. Microhabitat sampling locations were predominantly in Core Areas where 82% of nests and 73% of random locations occurred.

Nest-Random

Competitive models that best explained sage-grouse microhabitat nest selection included 12 predictor variables that described shrub characteristics, grass height, herbaceous canopy cover, and ground cover microhabitat characteristics (Table 3). In the nest-random modeling set, 73 models were competitive with the top model (ΔAIC_c = 0.25–3.96). The global model (K = 15, ΔAIC_c = 10.25) was not in the competitive model set. Model averaging indicated that the 95% confidence interval for the odds ratio estimate of Gap_{3m}, PerGrass_H, $Grass_{5m}$, $Forb_{1m}$, $BioCrust_{5m}$, and $Litter_{5m}$ overlapped 1 (Table 4); therefore, we considered those to be marginal predictor variables and limited our interpretations to primarily focus on the $Shrub_{1m}$, $Artr_{2.5m}$, Artr_H, $Gap_{0.5m}$, V0, and $BareRock_{5m}$ variables. Supported microhabitat variables encompassed all three microhabitat scales (1-m, 2.5-m, and 5-m). For every 10% increase in shrub cover at the 1-m scale ($Shrub_{1m}$), the relative probability of nest selection increased by approximately 48%. A 10% increase in big sagebrush cover within 2.5 m ($Artr_{2.5m}$) resulted in an increase in relative probability of nest selection by approximately 23%. For every 1 unit increase in the number of spaces between shrubs at the plot scale ($\geq$0.5 m and $<$1.0 m; $Gap_{0.5m}$) relative probability of nest selection increased by approximately 8%. Increased visual obstruction (VO) by 10 cm increased the relatively probability of nest selection by 28%.

Random-Random

Models that best explained microhabitat availability between Core and Non-Core Areas included 5 predictor variables (Table 3). The candidate model set consisted of 7 models (ΔAIC_c = 0.35–3.48). Model averaging indicated that the 95% confidence intervals for odds ratio estimates of the 5 predictor variables did not overlap 1 (Table 4). Therefore, our top model explaining microhabitat availability included the variables $Gap_{0.5m}$, $ResGrass_{1m}$, $Cactus_{1m}$, $BioCrust_{2.5–3.5m}$, and $Litter_{5m}$ at all 3 microhabitat scales. The number of shrub gap spaces ($\geq$0.5 m and $<$1.0 m; $Gap_{0.5m}$) and biological soil crust between 2.5 and 3.5 m away from the center of the transect ($BioCrust_{2.5–3.5m}$) were strong positive predictors of microhabitat availability in Core Areas. Residual grass cover within 1 m ($ResGrass_{1m}$) of center of random locations, cactus cover between 2.5 and 3.5 m away from the center of the transect, and

Table 3. Model comparisons of binomial generalized linear mixed models evaluating nest-site selection of sage-grouse (nest-random), availability of microhabitat within and outside of Core Areas (random-random), and sage-grouse use of microhabitat within and outside of Core Areas (nest-nest). Cox proportional hazard models were used to evaluate nest success of sage-grouse within and outside of Core Areas. Top five models for each analysis type were compared with Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w_i). Nests and random locations were located in five distinct study areas (n = 928 nests, n = 819 random locations, and n = 924 nests with survival data) throughout central and southwestern Wyoming, USA, 2008–2014.

	Model fit statistics			
Model[1]	**K**	**ΔAIC**	w_i	**Deviance**
Nest-random				
$Shrub_{1m}$ + $Artr_{2.5m}$ + Artr_H + $Gap_{0.5m}$ + VO + $BareRock_{5m}$	9	0.00	0.03	1965.12
$Shrub_{1m}$ + $Artr_{2.5m}$ + Artr_H + $Gap_{0.5m}$ + VO	8	0.25	0.03	1967.39
$Shrub_{1m}$ + $Artr_{2.5m}$ + $Gap_{0.5m}$ + VO + $BareRock_{5m}$	8	0.56	0.03	1967.70
$Shrub_{1m}$ + $Artr_{2.5m}$ + $Gap_{0.5m}$ + VO	7	1.07	0.02	1970.23
$Shrub_{1m}$ + $Artr_{2.5m}$ + Artr_H + $Gap_{0.5m}$ + Gap_{3m} + VO + $BareRock_{5m}$	10	1.25	0.02	1964.34
Null AIC_c = 400.13				
Random-random				
$Gap_{0.5m}$ + $ResGrass_{1m}$ + $Cactus_{1m}$ + $BioCrust_{2.5–3.5m}$ + $Litter_{5m}$	8	0.00	0.22	428.30
$Gap_{0.5m}$ + $ResGrass_{1m}$ + $Cactus_{1m}$	6	0.35	0.19	432.72
$Gap_{0.5m}$ + $ResGrass_{1m}$ + $Cactus_{1m}$ + $BioCrust_{2.5–3.5m}$	7	0.72	0.15	431.06
$Gap_{0.5m}$ + $ResGrass_{1m}$ + $Cactus_{1m}$ + $Litter_{5m}$	7	1.28	0.12	431.62
$Gap_{0.5m}$ + $ResGrass_{1m}$ + $BioCrust_{2.5–3.5m}$ + $Litter_{5m}$	7	1.82	0.09	432.16
Null AIC_c = 14.12				
Nest-nest				
Artr_H + $Gap_{0.5m}$ + $Bare_{5m}$	6	0.00	0.06	373.98
Artr_H + $Gap_{0.5m}$	5	0.01	0.06	376.02
Artr_H + $Gap_{0.5m}$ + $Bare_{5m}$ + $Rock_{5m}$	7	0.07	0.06	372.02
Artr_H + $Bare_{5m}$ + $Rock_{5m}$	6	0.57	0.05	374.54
Artr_H + $Gap_{0.5m}$ + $Rock_{5m}$	6	0.62	0.05	374.60
Null AIC_c = 3.30				
Nest success				
$ARTRpShr_{2.5m}$ + Gap_{2m} + $Rock_{2.5–3.5m}$	5	0.00	0.54	6056.86
$ARTRpShr_{2.5m}$ + Gap_{2m}	4	2.40	0.16	6063.43
Gap_{2m} + $Rock_{2.5–3.5m}$	4	3.11	0.11	6057.00
$ARTRpShr_{2.5m}$ + Gap_{2m}	4	3.55	0.09	6054.18
Gap_{2m}	3	4.60	0.05	6054.12
Null AIC_c = 9.74				

[1]Only the top five models and the null model are reported for each analysis type.

doi:10.1371/journal.pone.0150798.t003

litter within 5 m away from the transect center ($Litter_{5m}$) were all negative predictors of microhabitat availability in Core Areas. We report means and SE for microhabitat data at random locations within and outside of Core Areas nest-nest in S2 Table.

Nest-Nest

The models that explained nest site selection between Core and Non-Core Areas included 5 predictor variables across 31 models, including the null model (ΔAIC_c = 0.01–3.30). The null model was competitive with our top model—within 4 ΔAIC_c, which indicated that the top model was not much better at explaining differences between Core and Non-Core Area nests than the null model. The global model (K = 8, ΔAIC_c = 16.00) was not in the competitive

Table 4. Model-averaged parameter estimates and odds ratios with 95% confidence intervals (CI). Data were collected from five distinct study areas (n = 928 nests and n = 819 random locations) in central and southwestern Wyoming, USA, 2008–2014.

			95% CI			95% CI	
Parameter	**Estimate**	**SE**	**Lower**	**Upper**	**Odds ratio**	**Lower**	**Upper**
Nest-random							
Intercept	3.92						
$Shrub_{1m}$	0.04	0.01	0.03	0.05*	1.04	1.03	1.05*
$Artr_{2.5m}$	0.02	0.01	0.01	0.03*	1.02	1.01	1.03*
Artr_H	0.01	0.01	0.00	0.02*	1.01	1.00	1.02*
$Gap_{0.5m}$	0.08	0.01	0.05	0.11*	1.08	1.05	1.12*
Gap_{3m}	-0.08	0.08	-0.26	0.10	0.92	0.77	1.10
VO	0.02	0.01	0.01	0.03*	1.02	1.01	1.03*
PerGrass_H	0.01	0.01	-0.01	0.02	1.01	0.99	1.02
$Grass_{5m}$	-0.00	0.01	-0.02	0.02	1.00	0.98	1.02
$Forb_{1m}$	-0.00	0.01	-0.02	0.02	1.00	0.98	1.02
$BareRock_{5m}$	-0.01	0.01	-0.02	0.00*	0.99	0.98	1.00*
$BioCrust_{5m}$	0.01	0.02	-0.03	0.05	1.01	0.98	1.05
$Litter_{5m}$	0.00	0.01	-0.01	0.01	1.00	0.99	1.01
Random-random							
Intercept	10.57						
$Gap_{0.5m}$	0.38	0.10	0.19	0.56*	1.46	1.22	1.76*
$ResGrass_{1m}$	-0.16	0.04	-0.24	-0.07*	0.86	0.79	0.93*
$Cactus_{1m}$	-0.69	0.31	-1.30	-0.08*	0.50	0.27	0.92*
$BioCrust_{2.5–3.5m}$	0.17	0.08	0.01	0.34*	1.19	1.01	1.40*
$Litter_{5m}$	-0.03	0.02	-0.07	0.00*	0.97	0.94	1.00*
Nest-nest							
Intercept	10.29						
Artr_H	-0.03	0.02	-0.06	0.00*	0.97	0.94	1.00*
$Gap_{0.5m}$	0.16	0.10	-0.03	0.35	1.17	0.97	1.42
AnGrass	-0.08	0.06	-0.19	0.04	0.93	0.83	1.04
$Bare_{5m}$	0.06	0.04	-0.02	0.13	1.06	0.98	1.14
$Rock_{5m}$	-0.04	0.03	-0.10	0.02	0.96	0.90	1.02
Nest Success							
Gap_{2m}	-0.06	0.04	-013	0.01	0.95	0.87	1.01
$ARTRpShr_{2.5m}$	0.30	0.19	-0.07	0.67	1.35	0.93	1.96
$Rock_{2.5–3.5m}$	-0.01	0.01	-0.02	0.00*	0.99	0.98	1.00*

* Indicates 95% CI not overlapping 0 for beta estimates or 1 for odds ratios

doi:10.1371/journal.pone.0150798.t004

model set. Our top model comparing microhabitat differences between Core and Non-Core Areas included the variables Artr_H, $Gap_{0.5m}$, and $Bare_{5m}$. Model averaging indicated that the 95% confidence intervals for the odds ratio estimate of Artr_H did not overlap 1 (Table 4). Nests in Core Areas tended to have lower mean sagebrush height within 5 m of those nests compared to nests in Non-Core Areas. Model averaging indicated that the 95% confidence interval for the odds ratio estimates of $Gap_{0.5m}$, AnGrass, $Bare_{5m}$, and $Rock_{5m}$ overlapped 1 (Table 4); therefore, we considered those to be marginal predictor variables. We report means and SE for microhabitat data at nests within and outside of Core Areas nest-nest in S3 Table.

Nest Success

Average annual apparent nest success for all nests was 48.1% (444 hatched nests of 924), and the Kaplan-Meier nest success estimate for a 27-day incubation period was 42.0% (95% CI: 38.4–45.9%). No microhabitat variables in our final models violated the proportional hazards assumption of the Cox proportional hazards model. We did not find a difference in nest success between nests within and outside of Core Areas.

The top model describing nest success of sage-grouse included $ARTRpShr_{2.5m}$, Gap_{2m}, and $Rock_{2.5–3.5m}$. There were three other competitive models within $\Delta AIC_c = 2.40–3.55$ that included these variables (Table 3); thus, we model-averaged coefficient estimates. Model averaging indicated that $Rock_{2.5–3.5m}$ was the only variable to have model-averaged 95% CI of odds ratios that did not overlap 1 (Table 4). Although Gap_{2m} and $ARTRpShr_{2.5m}$ were considered in additive modeling, those variables were marginal predictors with model-averaged 95% CI of odds ratios overlapping 1 (Table 4). Therefore, we limited our interpretations to primarily focus on the $Rock_{2.5–3.5m}$ variable (Table 4). The top model included all variables considered in additive modeling, but was not the global model (i.e., model including all hypothesized variables). The null model was not competitive ($\Delta AIC_c = 9.74$) with models used in model averaging (Table 3). Rock cover between 2.5 and 3.5 m away from a nest ($Rock_{2.5–3.5m}$) was negatively associated with failure; thus, greater rock ground cover was associated with higher nest success (Table 4). We report means and SE for microhabitat data at successful and unsuccessful nests in S4 Table.

Discussion

Similar to other studies, we found that sage-grouse selected nesting habitat with greater concealment cover including sagebrush cover and height, and visual obstruction [7,9,14,15]. We found a positive association between nest selection and perennial grass height; however, this relationship had marginal support. Microhabitat characteristics associated with less bare ground and rock cover were not selected for compared to random locations. Females selected for more small gaps between shrubs (gap sizes $\geq$0.5 m and $<$1.0 m; $Gap_{0.5m}$). Locations with more small gaps but few large gaps may indicate 1) areas with greater homogeneity in shrub cover with more sagebrush distributed across the plot (i.e., no large holes in cover) or 2) provide adequate concealment while simultaneously allowing the female to detect and escape from predators.

From our random-random analyses, the availability of small gaps between shrubs was the only shrub variable that differed within and outside of Core Areas, with Core Areas having greater availability of small gaps. Core Areas had lower availability of residual grass and litter cover. This may be related to greater livestock grazing in these areas [e.g., 48], but we do not have data to support this and Wyoming's Core Area Policy does not include any measures that alter livestock grazing in Core Areas. Randomly available locations in Core Areas had more biological soil crust indicating areas with better soil stability. However, biological soil crusts can be compromised by excessive livestock trampling, especially during the growing season when crusts are not frozen [49], suggesting that grazing may not be reducing residual grass and litter in Core Areas compared to nearby non-Core Areas.

Sage-grouse use of microhabitat within and outside of Core Areas (nest-nest analysis) indicated that nests within Core Areas had lower big sagebrush height. Sage-grouse nests within Core Areas had shorter sagebrush heights, which may be associated with differing composition of sagebrush species. For instance, sage-grouse nests in the Jeffrey City study area primarily occurred in Core Area in Wyoming big sagebrush communities, whereas nests in the Bighorn Basin study area often occurred outside of Core Areas in taller mountain big sagebrush

communities. We found little support to suggest that annual grass, bare ground, and rock cover were predictive of nests within and outside Core Areas. Albeit, annual grasses are an important indicator of the resistance and resilience of sage-grouse habitats to respond to disturbance [50]. In addition, nest sites selected by sage-grouse in the Atlantic Rim and Stewart Creek of south-central Wyoming were negatively correlated with the presence of cheatgrass (*Bromus tectorum*), but positively correlated with greater perennial grass cover, litter, sagebrush cover, and visual obstruction [7].

Most of our microhabitat sampling locations were in Core Areas (82% of nests and 73% of random locations); however, we found little supporting evidence that Wyoming's Core Area Policy increased the availability of quality microhabitat for sage-grouse between 2008 and 2014. Because the Core Area Policy is relatively new and the primary focus of this policy is on landscape scale conservation—such as limits on oil and gas development—and not on anthropogenic activities more likely to affect microhabitat conditions such as grazing, it is not surprising that we only detected a slight difference. We found some differences in microhabitat characteristics within and outside Core Areas, but these differences were relatively minor relative to a landscape scale conservations policy. Also, our microhabitat sampling locations outside of Core Areas were adjacent to Core Areas (mean distance from Core Areas = 3.1 km [SD = 2.3] km with range of 0.04–12.0 km). Many of our locations outside of Core Areas had not been subject to greater surface disturbance than locations within Core Areas, and we did not continually monitor in landscapes being actively developed for more than 4 years. Thus, our sampling locations (nest and random locations) within and outside of Core Areas were generally in similar habitats.

The connection between specific microhabitat characteristics and nest success has not been consistently documented. Our nest success results need to be interpreted as effects of microhabitat characteristics within the range of what sage-grouse selected compared to what was available to them. Rock cover in our study areas was composed mainly of small diameter gravel $<$3 cm. It is possible nest placement within areas of greater rock ground cover may be a conferred adaptive advantage related to female concealment during incubation. Female sage-grouse have cryptic grayish-brown plumage [51] that may conform to nesting areas with a high percent of rock ground cover, which could lead to a lower probability of being discovered by visual predators. Nests with greater rock ground cover could also be correlated with areas closer to ridgelines that tend to be less traveled by olfactory predators, which tend to utilize drainage bottoms [52].

Although a marginal finding, we found that nests with greater heterogeneity in shrub species within 2.5 m of a nest were more successful, which could be related to areas with greater vegetative productivity. While most sage-grouse nests are found under sagebrush species [17], Musil [53] found that sage-grouse used shrub species other than big sagebrush more than expected in Idaho. Contrary to our expectations, sage-grouse had higher nest success at nests with more $\geq$2 m and $<$3.0 m (Gap_{2m}) gaps between shrubs within 5 m of the nest and more rock cover between 2.5 and 3.5 m away from a nest; however, this variable was a marginal finding with 95% CI of odds ratios overlapping 1. This finding is bounded by our results illustrating that sage-grouse selected areas with fewer large gaps. The olfactory ability of mammals is impeded by more updrafts and greater wind turbulence at the microhabitat-scale, and both of these climatic conditions are more likely to occur in areas with local heterogeneity in vegetation height [52]. Conover et al. [54] did not find any differences in updrafts or wind turbulence between nest and random or successful and unsuccessful sage-grouse nests. However, they only tested wind conditions directly above the nest or random location. There may be a nest success trade-off between areas with greater visual obstruction (where sage-grouse typically choose to place their nests) and areas with better olfactory obstruction near the nest (nests with

more medium sized gaps within 5 m of the nest that create local updrafts and allow for higher wind velocities near the nest); however, this is an untested hypothesis. Alternatively, there may be a potential correlation of this size gap with a microhabitat characteristic that was not measured (e.g., micro-scale topography, etc.).

Although general trends did emerge, we found few differences between microhabitat selection by sage-grouse within and outside of Core Areas, and no difference in nest success. Sage-grouse selected nests with greater concealment cover, and we found little evidence to suggest that there were differences in concealment cover at available habitats or nest sites in and outside of the Core Areas that were assessed. In addition, we found no evidence that concealment cover was important for nest success in our study areas. The Core Area Policy was designed to reduce negative impacts to quality sage-grouse breeding habitat [21], but our results suggest that the policy may primarily operate at larger spatial scales. As resource selection is a function of available habitats [55], changes in habitat quality may be manifested through management practices resulting in vegetative changes through time. Sage-grouse are a landscape species, with studies demonstrating that both nest selection and success are influenced by habitat characteristics at multiple spatial scales [6,16,56,57]. It is possible that changes in habitat quality at larger spatial scales would eventually have cascading effects on microhabitat quality. Continued assessment of differences in available habitat and nest success will be important steps to assess the viability of Wyoming's Core Area Policy. We found strong evidence that conservation of sage-grouse needs to maintain the availability of concealment cover at the microhabitat spatial scale for nesting. The inclusion of microhabitat information in sage-grouse conservation strategies will help management agencies better understand the relationships between fine scale microhabitat attributes and how those attributes influence sage-grouse nest selection, nest success, and ultimately habitat quality.

Supporting Information

S1 Table. Nest-random microhabitat data. Mean habitat characteristics (± SE) sampled within 5 m of nest and random locations for nest-random comparison in 5 study areas in central and southwestern Wyoming, USA, 2008–2014.
(DOCX)

S2 Table. Nest-random microhabitat data. Mean habitat characteristics (± SE) sampled within 5 m of nest and random locations for nest-random comparisons in 5 study areas in central and southwestern Wyoming, USA, 2008–2014.
(DOCX)

S3 Table. Nest-random microhabitat data. Mean habitat characteristics (± SE) sampled within 5 m of nest locations within and outside of Core Areas for nest-nest comparisons in 5 study areas in central and southwestern Wyoming, USA, 2008–2014.
(DOCX)

S4 Table. Nest-random microhabitat data. Mean habitat characteristics (± SE) sampled within 5 m of successful and unsuccessful nest locations in 5 study areas in central and southwestern Wyoming, USA, 2008–2014.
(DOCX)

S5 Table. Nest and random location microhabitat data. Microhabitat data for random and nest locations. Nest data includes data on nest survival.
(CSV)

Acknowledgments

Research funding was provided by the American Colloid Company; Anadarko Petroleum Corporation; Bates Hole, Bighorn Basin, South-Central, Southwest, and Wind River/Sweetwater River Local Sage-Grouse Working Groups; Jack H. Berryman Institute; Lincoln County Predator Management Board; Margaret and Sam Kelly Ornithological Research Fund; Predatory Animal District of Sweetwater County; School of Energy Resources and Wyoming Reclamation and Restoration Center at the University of Wyoming; Uinta County Predator Management Board; Utah Agricultural Experiment Station; Wyoming Animal Damage Management Board; Wyoming Sage-grouse Conservation Fund of the Wyoming Game and Fish Department; and the Wyoming Wildlife and Natural Resource Trust. Funding for analysis and publication of this paper was provided by the State of Wyoming Legislature through the Wyoming Wildlife and Natural Resource Trust on behalf of the Wyoming Sage-Grouse Implementation Team. This work would not have been possible without the help of many research technicians who assisted with capture, radio-tracking, and microhabitat sampling, and cooperation of many landowners throughout Wyoming for allowing access to private lands.

Author Contributions

Conceived and designed the experiments: JBD KTS JLB MRC CPK ACP. Performed the experiments: JBD KTS CPK ACP. Analyzed the data: JBD KTS. Contributed reagents/materials/analysis tools: JLB MRC. Wrote the paper: JBD KTS CPK ACP JLB MRC.

References

1. Connelly JW, Reese KP, Wakkinen WL, Robertson MD, Fischer RA. Sage grouse ecology. Idaho Department of Fish and Game Job Completion Report W-160-R-19, Boise, USA; 1994.
2. Braun CE. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies. 1998; 78:139–156.
3. Connelly JW, Hagen CA, Schroeder MA. Characteristics and dynamics of greater sage-grouse populations. In: Knick ST, Connelly JW, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology. Berkeley: University of California Press. 2011; pp 53–67.
4. Wallestad RO, Pyrah DB. Movement and nesting of sage grouse hens in central Montana. J Wildl Manage. 1974; 38:630–633.
5. Connelly JW, Reese KP, Schroeder MA. Monitoring of greater sage-grouse habitats and populations. Moscow: University of Idaho. 2003; Experiment Station Bulletin 80.
6. Doherty KE, Naugle DE, Walker BL. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. J Wildl Manage. 2010; 74:1544–1553.
7. Kirol CP, Beck JL, Dinkins JB, Conover MR. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. Condor. 2012; 114:75–89.
8. Gregg MA, Crawford JA, Drut MS, DeLong AK. Vegetational cover and predation of sage-grouse nests in Oregon. J Wildl Manage. 1994; 58:162–166.
9. Holloran M J, Heath BJ, Lyon AG, Slater SJ, Kuipers JL, Anderson SH. Greater sage-grouse nesting habitat selection and success in Wyoming. J Wildl Manage. 2005; 69:638–649.
10. Kaczor NW. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern M.Sc. Thesis, South Dakota State University. 2008. Available: https://gfp.sd.gov/hunting/docs/sagegrouse-nestbroodrearing.pdf.
11. Coates PS, Delehanty DJ. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. J Wildl Manage. 2010; 74:240–248.
12. Dinkins JB. Common raven density and greater sage-grouse nesting success in southern Wyoming: potential conservation and management implications. Ph.D. Dissertation, Utah State University. 2013. Available: http://digitalcommons.usu.edu/etd/1700/.
13. Hagen CA. Predation on greater sage-grouse: facts, process, and effects. In: Knick ST and Connelly JW, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Berkeley: University of California Press. 2011; pp 95–100.

14. Aldridge CL, Boyce MS. Linking occurrence and fitness to persistence: habitat based approach for endangered greater sage-grouse. Ecol Appl. 2007; 17:508–526. PMID: 17489256

15. Kolada EJ, Sedinger JS, Casazza ML. Nest site selection by greater sage-grouse in Mono County, California. J Wildl Manage. 2009; 73:1333–1340.

16. Dinkins JB, Conover MR, Kirol CP, Beck JL, Frey SN. Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. Condor. 2014; 116:629–642.

17. Connelly JW, Wakkinen WL, Apa AD, Reese KP. Sage-grouse use of nest sites in southeastern Idaho. J Wildl Manage. 1991; 55:521–524.

18. Webb SL, Dzialak MR, Harju SM, Winstead JB, Lockman D. Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human altered environments. Ecol Process. 2012; 1:15.

19. Doherty KE, Naugle DE, Tack JD, Walker BL, Graham JM, Beck JL. Linking conservation actions to demography: grass height explains variation in greater sage-grouse nest survival. Wildlife Biol. 2014; 20:320–325.

20. State of Wyoming. Office of Governor Freudenthal. State of Wyoming Executive Department Executive Order. Greater Sage Grouse Area Protection; 2008.

21. Doherty KE, Naugle DE, Copeland H, Pocewicz A, Kiesecker J. Energy development and conservation tradeoffs: systematic planning for sage-grouse in their eastern range. In: Knick ST, Connelly JW, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Volume 38. Berkeley: University of California Press. 2011; pp 505–516.

22. Copeland HE, Pocewicz A, Naugle DE, Griffiths T, Keinath D, Evans J, et al. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS ONE 8:e67261. doi: 10.1371/journal.pone.0067261 PMID: 23826250

23. Rodemaker EJ, Driese KL. Mapping Land Cover Types Using Remote Sensing, GIS, and Aerial Photography for the SW Wyoming, Pinedale and Green River, Wyoming Game and Fish Dept. Regions. Final Report to the Wyoming Game and Fish Dept. Wyoming Geographic Information Science Center, Laramie; 2006.

24. Holloran MJ, Anderson SH. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor. 2005; 107:742–752.

25. Giesen KM, Schoenberg TJ, Braun CE. Methods for trapping sage grouse in Colorado. Wildl Soc Bull. 1982; 10:224–231.

26. Wakkinen WL, Reese KP, Connelly JW, Fischer RA. An improved spotlighting technique for capturing sage grouse. Wildl Soc Bull. 1992; 20:425–426.

27. Eng RL. A method for obtaining sage grouse age and sex ratios from wings. J Wildl Manage. 1955; 19:267–272.

28. Dalke PD, Pyrah DB, Stanton DC, Crawford JE, Schlatterer EF. Ecology, productivity, and management of sage grouse in Idaho. J Wildl Manage. 1963; 27:810–841.

29. Northwest GAP Analysis Project. Land cover data (Gap Analysis Program Northwest) 30 m for Wyoming. Portland: Sanborn Map; 2008.

30. Aldridge CL, Boyce MS. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. Isr J of Ecol and Evol. 2008; 54:389–419.

31. Patterson RL. The sage grouse in Wyoming. Denver: Wyoming Game and Fish Commission and Sage Books; 1952.

32. Canfield RH. Application of the line interception method in sampling range vegetation. J Forestry. 1941; 39:388–394.

33. Wambolt CL, Frisina MR, Knapp SJ, Frisina RM. Effect of method, site, and taxon on line-intercept estimates of sagebrush cover. Wildl Soc Bull. 2006; 34:440–445.

34. Robel RJ, Briggs JN, Dayton AD, Hulbert LC. Relationship between visual obstruction measurements and weight of grassland vegetation. J Range Manage 1970; 23:295–297.

35. Griffith B, Youtie BA. Two devices for estimating foliage density and deer hiding cover. Wildl Soc Bull. 1988; 16:206–210.

36. Daubenmire R. A canopy-coverage method of vegetational analysis. Northwest Science. 1959; 33:43–64.

37. Anderson DR. Model based inference in the life sciences: a primer on evidence. New York: Springer Science; 2008.

38. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2013. Available: http://www.r-project.org/.
39. Burnham KP, Anderson DR. Model selection and multi-model inference: a practical information-theoretic approach. 2nd edition. New York: Springer-Verlag; 2002.
40. Arnold TW. Uninformative parameters and model selection using Akaike's information criterion. J Wildl Manage. 2010; 74:1175–1178.
41. Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. Evaluating resource selection functions. Ecol Model. 2002; 157:281–300.
42. PRISM Climate Group, Oregon State University. Available: http://prism.oregonstate.edu, created 10 July 2015.
43. Manly BF, McDonald LL, Thomas DL, McDonald TL, Erickson WP. Resource selection by animals: statistical design and analysis for field studies. London: Chapman and Hall; 2002.
44. Cox DR. Regression models and life-tables. J R Stat Soc Series B Stat Methodol. 1972; 34:187–220.
45. Hosmer DW, Lemeshow S. Applied survival analysis: regression modeling of time to event data. New York: John Wiley and Sons; 1999.
46. Therneau TM, Gambsch PM. 2000. Modeling survival data: extending the Cox model. New York: Springer-Verlag; 2000.
47. Kaplan EL, Meier P. Nonparametric estimation from incomplete observations. J American Statistical Association 1958; 53:457–481.
48. Boyd CS, Beck JL, Tanaka JA. Livestock grazing and sage-grouse habitat: impacts and opportunities. J Range Appl. 2014; 1:58–77.
49. Memmott KL, Anderson VJ, Monsen SB. Seasonal grazing impact on cryptogamic crusts in a cold desert ecosystem. J Range Manage. 1998; 51:547–550.
50. Chambers JC, Pyke DA, Maestas JD, Pellant M, Boyd CS, Campbell SB, et al. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 2014; General Technical Report RMRS-GTR-326.
51. Schroeder MA, Young JR, Braun CE. Sage grouse (*Centrocercus urophasianus*). Pages 1–28 *in* A. Poole and F. Gill, editors. The birds of North America, No. 425. The Birds of North America, Philadelphia, Pennsylvania: 1999.
52. Conover MR. Predator–prey dynamics: the use of olfaction. Boca Raton: Taylor and Francis; 2007.
53. Musil DD. Use of dwarf sagebrush by nesting greater sage-grouse. In: Sandercock BK, Martin K, editors. Ecology, Conservation, and Management of Grouse. Studies in Avian Biology Berkeley: University of California Press. 2011; pp 119–136.
54. Conover MR, Borgo JS, Dritz RE, Dinkins JB, Dahlgren DK. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. Condor. 2010; 112:331–336.
55. Thomas DL, Taylor EJ. Study designs and tests for comparing resource use and availability II. J Wildl Manage 2006; 70:324–330.
56. Dinkins JB, Conover MR, Kirol CP, Beck JL, Frey SN. Greater sage-grouse (*Centrocercus urophasianus*) hen survival: effects of raptors, anthropogenic and landscape features, and hen behavior. Can J Zool. 2014; 92:319–330.
57. Kirol CP, Beck JL, Huzurbazar SV, Holloran MJ, Miller SN. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecol Appl. 2015; 25:968–990. PMID: 26465037

Freshwater Biology

Freshwater Biology (2016) doi:10.1111/fwb.12721

Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams

ALAN LAW, FIONA MCLEAN AND NIGEL J. WILLBY

Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, U.K.

SUMMARY

1. Small-scale discontinuities, formed by accumulations of wood, are recognised as a key feature of functionally intact forested streams because they promote organic matter retention, increase habitat complexity and provide flow refugia. Re-establishing such features in physically degraded streams is therefore a common priority for restoration schemes. Ecosystem engineering by beavers in the form of dam building might offer a natural mechanism for restoring degraded streams. Despite an increase in beaver reintroductions globally, the ecosystem engineering concept has rarely been applied to restoring biodiversity and ecosystem function, especially within degraded freshwater systems.
2. By comparing multiple beaver-modified and unmodified sites on headwater streams draining 13 ha of pastureland in eastern Scotland, U.K., we investigated if hydromorphological changes caused by reintroduced beavers (*Castor fiber*) translate into desirable biological responses when there is a long history of physical degradation and contraction of the regional species pool due to agricultural land use.
3. Beaver modified in-stream habitat by constructing 10 dams, thus creating a series of interconnected dam pools. Organic matter retention and aquatic plant biomass increased (7 and 20 fold higher respectively) in beaver ponds relative to unmodified channels, consistent with the lower fluctuation in stream stage observed below a series of dams. Growing season concentrations of extractable P and NO_3 were on average 49% and 43% lower respectively below a series of dams than above, although colour and suspended solids concentrations increased.
4. Macroinvertebrate samples from beaver-modified habitats were less taxon rich (alpha diversity on average 27% lower) than those from unmodified stream habitat. However, due to significant compositional differences between beaver versus unmodified habitats, a composite sample from all habitats indicated increased richness at the landscape scale; gamma diversity was 28% higher on average than in the absence of beaver-modified habitat. Feeding guild composition shifted from grazer/scraper and filter feeder dominance in unmodified habitats to shredder and collector-gatherer dominance in beaver-created habitats.
5. Dam building by beaver in degraded environments can improve physical and biological diversity when viewed at a scale encompassing both modified and unmodified habitats. By restoring ecosystem processes locally, it may also offer wider scale benefits, including greater nutrient retention and flood attenuation. These benefits should be evaluated against evidence of any negative effects on land use or fisheries.

Keywords: *Castor fiber*, diversity, habitat heterogeneity, macroinvertebrates, restoration

Introduction

Small-scale discontinuities in streams caused by the accumulation of large wood (snags, logjams, woody debris dams) are recognised as an important natural component of functionally intact forested streams (Gurnell, Piegay & Swanson, 2002). Historically, these features have often been removed to improve drainage and flood

Correspondence: Alan Law, Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, U.K. E-mail: alan.law1@stir.ac.uk

© 2016 John Wiley & Sons Ltd

conveyance. Their reinstatement is therefore often prioritised when restoring physically degraded streams (Poole, 2002). Beavers (*Castor fiber* and *Castor canadensis*) have experienced a substantial global population increase over the last century aided by protection and reintroduction programmes. Beaver have been advocated as a possible option for restoring ecologically degraded systems (Nolet & Rosell, 1998; Pollock *et al*., 2014), reflecting their potential to create and re-establish natural discontinuities and unique habitats via dam building (Naiman & Rogers, 1997). Systems that are likely to benefit include forested stream channels from first to fourth order (Harthun, 1999; Burchsted *et al*., 2010), arid and semi-arid environments (Gibson & Olden, 2014) and wetlands (Wright, Jones & Flecker, 2002; Elmeros, Madsen & Berthelsen, 2003; Sjöberg & Ball, 2011). However, reintroducing long-extinct species such as beavers to densely populated regions is also controversial; experience suggests that this can increase human–wildlife conflict and the need for intervention (Nolet & Rosell, 1998; Siemer *et al*., 2013).

By building dams, beaver raise and stabilise water levels, thus maintaining a submerged lodge or burrow entrance. This reduces predation risk while increasing access to inundated wooded riparian zones (Rosell *et al*., 2005). Beaver dams dissipate stream energy and slow flow, thereby altering hydraulic connectivity and discharge (Margolis, Raesly & Shumway, 2001a; Benke & Wallace, 2003). Ultimately, they transform sections of channel from erosional to depositional environments that act as a sink for plant propagules, nutrient-rich sediment and coarse organic matter (Anderson *et al*., 2014). Where dam integrity is maintained, the ponded area will also support extensive aquatic vegetation (Rolauffs, Hering & Lohse, 2001). Over decadal time scales, dam disintegration and pond drainage follow abandonment of a beaver territory, allowing colonisation of exposed sediments by terrestrial plants, thus forming 'beaver meadows' (Naiman, Johnston & Kelley, 1988). However, in more dynamic situations, where cycles of occupation by beaver are short and breaching and rebuilding of dams is common, smaller dam ponds interconnected by sections of running water will occur (Gurnell, 1998). Beaver dams therefore directly or indirectly modify various physical, hydraulic and chemical processes in streams, creating a mosaic of habitats and food resources (Hood & Larson, 2014a; Smith & Mather, 2013). This increased habitat heterogeneity generally has positive effects on a diverse range of biota including aquatic plants (McMaster & McMaster, 2001), macroinvertebrates (Margolis *et al*., 2001a), fish (Kemp *et al*., 2011), amphibians (Dalbeck, Luscher & Ohlhoff, 2007) and birds (Nummi & Holopainen, 2014).

Ponds formed by beaver are an additional and novel source of habitat heterogeneity that differ from other types of ponds and may support unique biological assemblages (Rolauffs *et al*., 2001; Willby *et al*. 2016). Beaver ponds are characterised by higher lateral connectivity than the rivers they modify, with beaver-created channels enlarging the aquatic–terrestrial interface (Hood & Larson, 2014b), and are intermittently disturbed through foraging, caching of woody material, maintenance of dams and fluctuating water levels. The associated physical structures, i.e. dams, lodges, food caches (submerged wood with higher surface areas than conventional large wood inputs) and channels, further increase habitat complexity (Clifford, Wiley & Casey, 1993; France, 1997; Hood & Larson, 2014a). The habitat-altering effects of beaver dams in natural, mostly forested environments have long been recognised (e.g. Sprules, 1941) and the resulting physicochemical changes in such streams are well studied (see reviews by Gurnell, 1998 and Rosell *et al*., 2005). Various authors have used macroinvertebrates as indicators of the effects of this habitat engineering (e.g. Clifford *et al*., 1993; France, 1997; Benke & Wallace, 2003; Anderson & Rosemond, 2007), reflecting ease of sampling and sensitivity of invertebrates to the changes in sediment and water velocity that accompany damming (Nummi, 1989). However, one particular question that is integral to the thinking behind the reintroduction of beavers globally, but has not been addressed in previous studies, is whether the ecosystem engineer concept (Jones, Lawton & Shachak, 1994) extends to restoring biodiversity and ecosystem function within degraded freshwater systems, especially in regions where beaver have long been absent. Streams and artificial habitats such as drainage ditches are common in anthropogenic landscapes, but mostly lack physical and biological diversity due to historical straightening, removal of blockages and encroachment by surrounding land use into the riparian zone. Flood attenuation, nutrient storage and support for biodiversity are therefore heavily compromised. Using beaver to restore habitat heterogeneity to anthropogenic landscapes without the need for physical habitat engineering by humans therefore offers multiple potential benefits. However, it will fall short of expectations if the transformation of physical habitat by beaver through ecosystem engineering is not matched biologically (Byers *et al*., 2006; Palmer, Hondula & Koch, 2014). This concern applies where beaver have been recently reintroduced (e.g. Belgium, Bosnia and Herzegovina, Croatia,

Denmark and Serbia; Halley, Rosell & Saveljev, 2012), but especially so where beaver have not yet been fully reintroduced (e.g. Britain) and where the potential merits of ecosystem engineering versus possible impacts on land use and fisheries are strongly contested.

Our study focused on the implications of beaver reintroduction for physicochemical processes and biodiversity in small agricultural streams, an extremely common but neglected habitat within the native range of Eurasian and North American beavers. We particularly assessed the associated changes in richness, abundance, composition and feeding function of aquatic macroinvertebrates. We evaluated (i) how the presence of beaver-modified habitats affects local and landscape-scale species richness and species accumulation rates; (ii) if species turnover increases between habitats when beaver-created habitats occur in the landscape; and (iii) whether the composition of invertebrate functional feeding groups in beaver-created and unmodified habitats is consistent with differences in their physicochemical properties.

Methods

Site and habitats

The study took place on a 13 ha site within a private estate of 525 ha near Blairgowrie, in eastern Scotland (56°37′32.81″N, 3°13′36.72″W). Blairgowrie receives approximately 820 mm of rain annually, and has a mean annual temperature of 8.4 °C (Meteorological Office UK, 2013). The study site, which is situated at an elevation of 200 m, is drained by a small spring-fed stream (the Burneished Burn), 0.5–2 m wide and 0.1–0.3 m deep, that runs for ~2 km through agricultural land used mostly for livestock grazing. The mean discharge of this stream at its outflow from the study site was 0.025 $m^3 s^{-1}$ in 2010–11 (Fiona McLean unpublished data). This stream and its minor tributaries were straightened and realigned prior to 1860. A mature conifer plantation (*Picea* spp. and *Larix* spp.) forms the southern edge of the catchment and a small block of deciduous woodland (*Betula pubescens*, *Salix* spp., *Alnus glutinosa* and *A. incana*) replanted in 1990 encloses the source. In 2002, a pair of adult Eurasian beaver, *Castor fiber*, was introduced to this stream by the landowner to assess the value of beavers for wetland creation. Breeding first occurred in 2005, and 3–6 animals have been present annually thereafter. Beaver first dammed the upstream section of channel in 2003 and subsequently built eight more dams (four upstream and four downstream of this original dam) over the next 3 years. A tenth structure was added in early summer 2011. The mean distance between dams was 53 ± 28 m (±SD, range = 20–600 m). The observed frequency of 5 dams km^{-1} of channel is within the range 0.14–22 dams km^{-1} reported from Russia and North America (Zavyalov, 2014).

Dam construction by beaver modified the surrounding habitat. Four discrete habitats were defined *a priori* for the purposes of sampling; (i) immediately upstream (0–3 m) of a dam (habitat US), (ii) the dam pond 5–10 m upstream from the dam (habitat VG), (iii) immediately downstream (0–3 m) of a dam (habitat DS) and (iv) unmodified sections of channel outwith the influence (>50 m) of the nearest dam on depth and flow (habitat UM) (Fig. 1). As unmodified sections of stream were not always present between successive beaver impoundments, samples from unmodified habitats were also collected from undammed tributary streams that were similar in terms of width, velocity, substrata and riparian characteristics. The mean hydrological distance of unmodified tributaries from any beaver activity was 317 ± 198 m (±SD, range = 100–650 m). Lentic conditions occurred in habitat US (mean water velocity = 0.2 cm s^{-1}, range = 0–3 cm s^{-1}), with high volumes of organic matter accumulating. This habitat was moderately disturbed due to beavers regularly maintaining dams with mud, rocks and cut branches, and in some cases, excavating burrows; submerged vegetation was therefore sparse. However, the dam structure itself often supported ruderal terrestrial plants, such as *Urtica dioica* and *Rumex obtusifolius*. Habitat VG was characterised by shallow (0.5–0.8 m deep), very slow moving waters (mean velocity = 0.1 cm s^{-1}, range = 0–1 cm s^{-1}) and extensive aquatic vegetation, the most abundant plant species being *Potamogeton natans*, *Callitriche stagnalis*, *Glyceria maxima*, *G. fluitans*, *Rorippa nasturtium-aquaticum*, *Myosotis scorpioides* and *Elodea canadensis*. Habitat DS was characterised by water flowing over and through the dam (mean velocity = 2.1 cm s^{-1}, range = 0–30 cm s^{-1}). Habitat UM was considered indicative of the conditions prior to dam construction (confirmed by visual assessments and archive photographs); water velocity ranged from 0 to 69 cm s^{-1} (mean = 15.8 cm s^{-1}), the stream bed comprised a mixture of sand and coarse gravel, and there was a sparse coverage of the moss *Fontinalis antipyretica*.

Physicochemical measurements

Paired water samples (0.75 L) for the period 23 June 2010 to 13 May 2011 were obtained using ISCO 3700 automatic water samplers placed upstream and down-

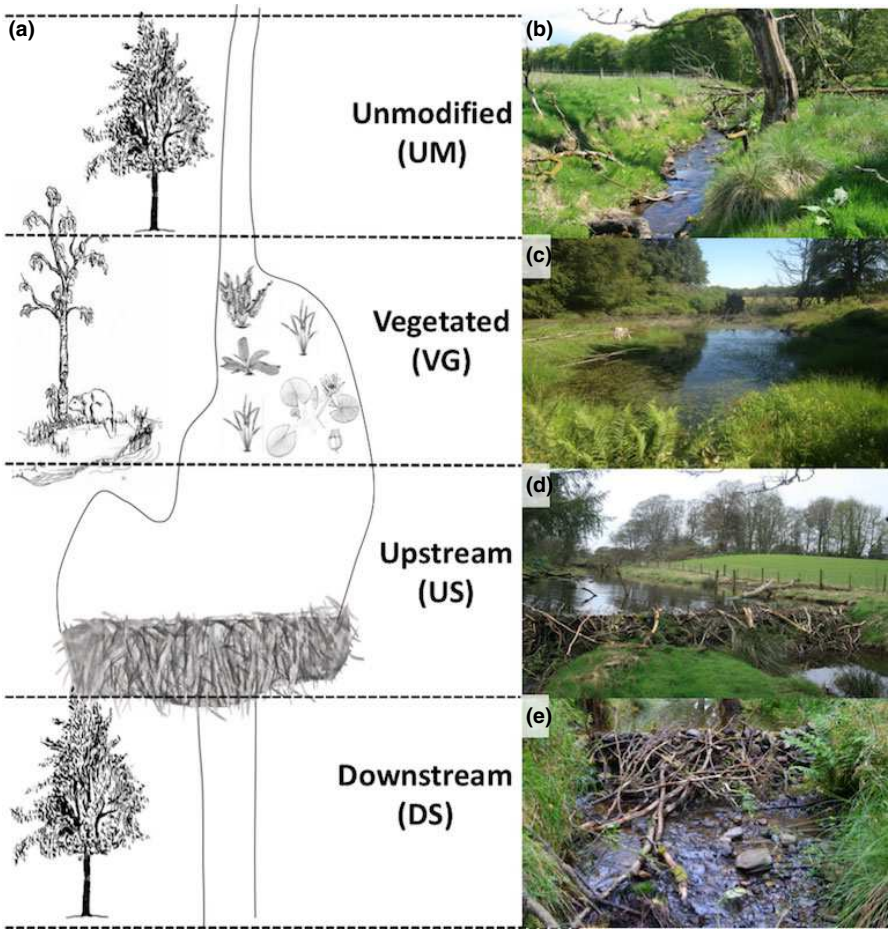


Fig. 1 A schematic diagram of the habitat types sampled in this study (a), in addition to photographs representative of these habitats; (b) a stream unmodified by beavers, (c) vegetated pond upstream of a beaver dam, (d) immediately upstream of a dam and (e) immediately downstream of a dam (all photos © N. Willby).

stream of a 500 m section of channel containing a series of four beaver dams. An integrated automatic stage (water level) recorder measured stage at each of these locations at 15 min intervals. Water samples were collected on a 12, 24 or 72 h cycle. Sampling was not flow proportionised, but was most frequent during periods when heavy rainfall was forecast and was reduced in the spring. No samples could be obtained during a prolonged period of sub-zero temperatures from 1 December 2010 to 1 March 2011. A total of 133 paired samples was collected and analysed for total suspended solids (TSS), colour, extractable P, nitrate, chloride and sulphate using standard techniques. TSS was determined from the weight of residue retained by pre-dried 1.2 μm glass microfibre filter papers. Colour was measured on a Thermo Spectronic Hellios Epsilon spectrophotometer as absorbance at 440 nm to provide an indication of dissolved organic carbon (DOC) (Pace & Cole, 2002). Extractable P was determined using the molybdenum blue method (Murphy & Riley, 1962). Concentrations of major anions were determined using a DIONEX, DX-120 Ion Chromatograph.

Samples of stream substrata (upper 5 cm) were collected in summer 2013 at randomly located positions in the four described habitat types: upstream and downstream of each of the 10 dams, and in unmodified habitats and vegetated habitats where present (total $n = 39$). Material was collected using a 10-cm diameter bottomless bucket and subsequently rinsed through sieves of mesh size 21.4 mm, 16 mm, 11.2 mm, 5.6 mm, 2 mm, 1 mm, 500 μm, 250 μm and 125 μm. Sieved material was dried at 80 °C for 24 h with the weight of the different size fractions being used to calculate substratum diversity and evenness. Dried samples were then aggregated to form coarse (1–21.4 mm) and fine (125–500 μm) fractions. The percentage of organic matter in each fraction was determined based on loss on ignition by burning 10 g of material in a pre-dried crucible at 550 °C for 24 h. Aquatic plant biomass per habitat was estimated by removing above-ground vegetation within replicate ($n = 7$) 20 cm × 20 cm quadrants placed randomly within each habitat. Samples were dried at 60 °C for 24 h and weighed. Replicate measures (×5) of water depth were made randomly within all sampling locations.

Macroinvertebrate sampling

Macroinvertebrates were sampled in spring (n = 35), summer (n = 37) and autumn (n = 37) 2011 within the four described habitat types. Differences in sample numbers between seasons reflect the construction of a dam between spring and summer sampling periods and the lack of vegetated habitat at three sites. All dam systems present on the site were sampled, including the nine dams constructed between 2002 and 2006, plus a further dam formed in summer 2011. Semiquantitative samples were collected for 1 min using a D-framed kick net (mesh size 500 μm), over a fixed area of 2 m^2, which encompassed the characteristic features of each habitat type. The net was swept through the water column, vegetation and any accumulated organic material to collect benthic, water surface and plant-associated organisms. When the stream bed was compacted, material was loosened by kicking and caught in a net placed immediately downstream. To minimise disturbance, only a single sample could be collected from each replicate example of each habitat on a given date. Samples were preserved using 70% denatured methylated spirit, sorted in the lab and identified to the highest practicable taxonomic resolution (see Table S1).

Treatment of data

Water-quality data were subdivided into growing season (May–September) and winter (October–April) periods. Variables were compared within seasons between habitats using a paired t-test with bootstrapping. Sediment organic matter content, Shannon's diversity Index (H'), Shannon's equitability (E_H) and aquatic plant biomass did not meet requirements for parametric analyses and therefore differences between habitats were analysed using Kruskal–Wallis tests with *post hoc* multiple comparisons. The absence of a satisfactory rating curve for the upstream monitoring station prevented stage being converted to discharge so the comparison of regime above and below the series of dams was limited to simple hydrological indicators such as time to peak stage and coefficient of variation in stage. Centralised stage (stage/median stage over the length of record) was used to compare the data from upstream and downstream stations while paired t-tests were used to evaluate differences in time to peak stage between stations.

Macroinvertebrate species richness was expressed as the number of taxon per sample or as H', with species evenness represented by E_H. Differences in species richness with respect to habitat, season and dam age were analysed using a generalised linear model with a Poisson error distribution and log-link function. Quasi-Poisson distributions were used to correct for overdispersion, as indicated in the results by a t value associated with each P-value, rather than the Z value given from a conventional Poisson distribution. To control for potential spatial pseudoreplication caused by unequal independence of replicates (due to beaver dams being distributed over the same stream system), the distance to furthest upstream sample was included as a term in these models. General linear models with *post hoc* multiple comparisons using Tukey's Honestly Significant Differences (HSD) were used to assess differences in macroinvertebrate H' and E_H between habitats within seasons, or within habitats between seasons. Macroinvertebrate H' and E_H were normalised prior to statistical analyses using a $\log_{10}$ $(x + 1)$ transformation. To compare the accumulation rates of species per habitat type, accumulation curves were generated using individual-based rarefaction (Colwell, Mao & Chang, 2004), as abundance varied strongly between samples and species richness is highly sensitive to the number of individuals present. Species richness was estimated using the abundance-based estimator of Chao (1987).

Species abundance data were log-transformed before being converted to a pairwise, sample-by-sample dissimilarity matrix, using a Bray–Curtis dissimilarity Index (BCI). Species composition and turnover per habitat and season were then compared using non-metric multidimensional scaling (NMDS). A permutational multivariate analysis of variance was used to test the effects of habitat, distance to closest upstream sample and season on composition, based on the BCI dissimilarity matrix. Species characteristic of particular habitats were identified using the Indicator Value method (Dufrêne & Legendre, 1997).

All taxa were assigned to functional feeding guilds (FFG) using Schmidt-Kloiber & Hering (2015) (http://www.freshwaterecology.info). As feeding often spanned multiple guilds, the total number of individuals per species per sample were distributed across the reported guilds based on a 10-point assignment system (Moog, 1995). Since trait data did not meet assumptions of parametric tests, a Kruskal–Wallis one-way analysis of variance with *post hoc* multiple comparison tests was used to assess differences in FFG composition between habitats within seasons, and within habitats between seasons.

Species rarity was measured using U.K. mainland distribution data from the National Biodiversity Network (NBN, 2014). A rarity score was derived from the reciprocal of the log number of hectads in which each species was recorded. The sample rarity score comprised the abundance weighted mean species rarity score, where abundance equated to the log number of individuals of

each species recorded. Therefore, high sample rarity scores represent a greater than average abundance of rare species. These data did not meet assumptions of parametric tests; therefore, a Kruskal–Wallis one-way analysis of variance with *post hoc* multiple comparison tests was used to assess species rarity scores between habitats.

All statistical analyses and graphics were produced using R Studio version 2.15.0 (R Development Core Team, 2013), with the additional packages; vegan (Oksanen *et al.*, 2013), plyr (Wickham, 2011), ecodist (Goslee & Urban, 2007), sciplot (Morales *et al.*, 2011), labdsv (Roberts, 2010) and fossil (Vavrek, 2011).

Results

Physicochemical characteristics

Differences in water chemistry above and below the series of dams were most pronounced during the growing season. Downstream reductions in summer concentrations of P and N (Table 1) were especially marked (49% and 43% respectively), while colour was on average twice as high downstream of monitoring stations. Suspended solids were higher downstream of monitoring stations throughout the year (by an average of 5.8 fold). Vegetated and upstream habitats were both deeper and had a higher percentage of coarse and fine substrate organic matter content (total organic matter content seven fold higher) than downstream and especially unmodified habitats (Table 2). Higher velocity downstream and unmodified habitats had the greatest substratum diversity, with unmodified samples being the most uneven. Vegetated habitats had a significantly greater aquatic plant biomass (~20 times higher) than unmodified habitats. Up- and downstream habitats had zero plant biomass.

Paired recording of stage from November 2010 to May 2011 above and below a 500 m section of channel containing a series of four dams captured nine peak run-off events (Fig. 2). The time to peak stage downstream of the dams during these events (34.6 ± 7.7 hours; mean ± SE) was longer than at the upstream position (29.4 ± 5.6 hours; mean ± SE), but not significantly so ($P = 0.17$). As a consequence of peak stage attenuation, the variation in stage was substantially lower below the dams compared to above them (coefficient of variation in stage = 0.22 and 0.62 respectively).

Macroinvertebrate richness and abundance

In total, 109 invertebrate samples were taken across three seasons with 156 taxa recorded from the 84,520

Table 1 Summary of mean water chemistry by season and habitat (mean ± SE) from upstream and downstream of a section of a channel containing four beaver dams.

	Summer ($n = 61$)		Winter ($n = 72$)	
	Upstream	Downstream	Upstream	Downstream
Total suspended solids (mg L^{-1})	15.11 ± 2.71	85.68 ± 17.86*	11.77 ± 2.86	43.29 ± 5.06**
Colour @ 440 nm	0.07 ± 0.01	0.14 ± 0.01***	0.05 ± 0.00	0.06 ± 0.00
Extractable P (μg L^{-1})	43.09 ± 4.53	22.13 ± 1.48**	23.10 ± 2.44	18.31 ± 2.06
Nitrate (mg L^{-1})	5.50 ± 0.39	3.12 ± 0.12**	5.05 ± 0.21	5.02 ± 0.24
Chloride (mg L^{-1})	6.92 ± 0.27	5.57 ± 0.06**	5.93 ± 0.24	5.98 ± 0.30
Sulphate (mg L^{-1})	3.13 ± 0.32	3.58 ± 0.16*	5.79 ± 0.19	5.63 ± 0.21

Asterisks indicate significant differences obtained from paired t-tests with bootstrapping ($P < 0.001$ ***, < 0.01 **, < 0.05 *).

Table 2 Physical characteristics and sediment structure and diversity per habitat, as mean ± SE (min-max).

	VG	US	DS	UM	
Water depth (cm)	47.8 ± 3.7^{a} (12–78)	54.0 ± 3.9^{a} (15–100)	13.2 ± 2.2^{b} (1–49)	6.5 ± 0.5^{b} (2–14)	***
Coarse (>1 mm) organic matter content (%)	25.4 ± 3.6^{a} (11.3–45.6)	24.0 ± 4.4^{a} (8.5–51.6)	7.5 ± 3.9^{b} (1.0–41.2)	3.0 ± 0.7^{b} (1.3–6.2)	***
Fine (<1 mm) organic matter content (%)	18.5 ± 2.5^{a} (5.7–29.5)	18.1 ± 3.0^{a} (7.9–36.7)	8.2 ± 4.9^{b} (0.0–50.4)	3.1 ± 0.6^{b} (1.2–5.4)	***
Particle size diversity (H')	1.24 ± 0.05^{a}	1.35 ± 0.05^{ad}	1.70 ± 0.04^{bc}	1.52 ± 0.03 ^{cd}	***
Particle size equitability (E_H)	0.88 ± 0.02^{a}	0.87 ± 0.03^{a}	0.80 ± 0.03^{ac}	0.65 ± 0.02^{bc}	***
Plant biomass (DW g m^{-2})	554.9 ± 60.4^{a} (329.0–835.8)	0	0	27.84 ± 18.5^{b} (0–117.9)	**

Abbreviations; VG – vegetated, US – upstream, DS – downstream and UM – unmodified. Asterisks indicate significant differences obtained from Kruskal-Wallis tests ($P < 0.001$ ***, < 0.01 **, < 0.05 *). Numbers sharing the same superscript are not significantly different ($P > 0.05$).

individuals collected (Table 3). Vegetated (43.0%) and upstream (21.2%) habitats contributed most individuals to the total abundance, followed by unmodified (18.9%) and downstream habitats (16.9%). Unmodified habitats had significantly greater mean species richness per sample compared to downstream, upstream and vegetated habitats respectively (DS; $t_{104} = -3.58$, $P < 0.001$, US; $t_{104} = -5.06$, $P < 0.001$, VG; $Z_{104} = -2.00$, $P = 0.048$). Of the beaver-modified habitats, vegetated habitats had the greatest mean species richness (Table 3).

Distance to the furthest upstream sample did not significantly affect mean species richness ($t_{108} = 0.66$, $P = 0.512$), indicating that habitat effects were local and unchanged by upstream dams. Beaver-created habitats associated with the recently constructed dam (<1 year old) generally had a lower mean richness (VG = 13, US = 12, DS = 16) than habitats from older dams (4–8 years old, $n = 9$, VG = 19, US = 14, DS = 16), but these differences were not significant (VG; $t_{20} = -1.25$, $P = 0.228$, US; $Z_{28} = -0.88$, $P = 0.378$, DS; $Z_{28} = -0.29$, $P = 0.769$).

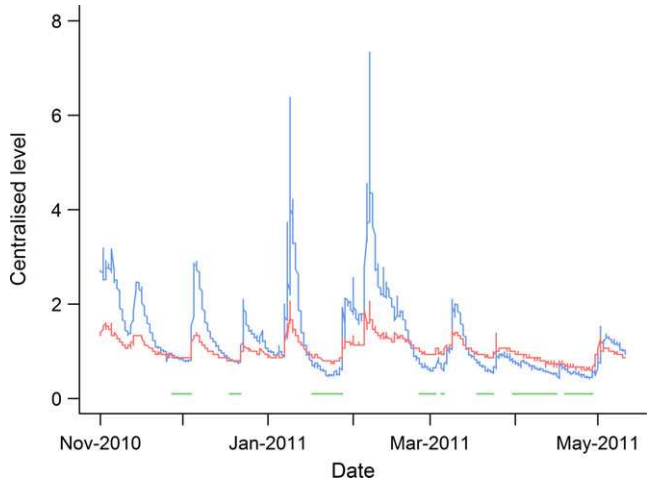


Fig. 2 Short-term variation in centralised stage upstream (blue line) and downstream (red line) of a section of channel containing four beaver dams. Periods of dry weather flow are shown in green.

The greatest diversity (H') occurred in unmodified and to a lesser extent downstream habitats (Table 3). Significant seasonality in diversity within habitats occurred only within upstream sites, where spring samples had a greater mean diversity than summer or autumn ($F_{2,26} = 6.33$, $P = 0.006$; Table S2). Community evenness (E_H) was similar across upstream, downstream and unmodified habitats, but was markedly lower in vegetated habitats. Within-habitats, diversity in samples from the vegetated habitat was consistently least even, especially in the summer. The range of rarity scores was narrow (0.35–0.38), thus indicating similar levels of ubiquity of taxa in all habitats.

At the lowest rarefied number of individuals per habitat (effectively a measure of alpha diversity corrected for sampling effort), unmodified sites were more species rich than any beaver-modified habitats by an average of 11 species (range: 5–16 species) (Fig. 3). Of the beaver-influenced habitats, upstream and vegetated habitats had the lowest taxon accumulation rates. Downstream habitats displayed most seasonal variation in accumulation rate, with summer being notably less taxon rich than spring or autumn, although in comparison to other beaver-modified habitats, downstream areas still had the highest accumulation rates regardless of season (Fig. S1). In all habitat types, the individual-based taxon accumulation curve rarely reached a plateau, implying that further sampling would yield more species, perhaps related to habitat heterogeneity within individual habitats. However, observed richness averaged 87.1 ± 1.6% of computed richness, based on the 12 habitat x season combinations, indicating that sampling of the fauna was largely and

Table 3 Summary of macroinvertebrate data by habitat (mean ± SE).

	VG (n = 21)	US (n = 29)	DS (n = 29)	UM (n = 30)		Aggregate (n = 109)
Mean sample richness (range)	18.2 ± 1.3^{a} (6–27)	14.3 ± 0.9^{b} (8–27)	16.3 ± 1.0^{ab} (5–33)	21.9 ± 1.0^{c} (11–32)		17.7 ± 0.6 (5–32)
Total richness	86	80	97	90		156
Abundance-based species estimator	98	106	112	106		167
Mean species rarity	0.35^{a}	0.36^{a}	0.36^{a}	0.38^{b}	***	0.36
Mean individuals per sample (range)	1741.9 ± 404.5^{a} (274–7344)	620.6 ± 86.5^{b} (153–2156)	496.2 ± 68.4^{b} (47–1226)	536.2 ± 77.8^{b} (153–1840)	***	780.3 ± 95.9 (47–7344)
Total individuals	36,579	17,997	14,390	16,085		85,051
Shannon's diversity (H)	4.9 ± 0.4^{a}	5.3 ± 0.3^{a}	5.8 ± 0.3^{a}	7.9 ± 0.4^{b}	***	5.6 ± 0.2
Shannon's equitability (E_H)	0.27 ± 0.02^{a}	0.36 ± 0.02^{b}	0.36 ± 0.02^{b}	0.36 ± 0.02^{b}	**	0.33 ± 0.01

Abbreviations for habitat codes are; VG – vegetation, US – upstream, DS – downstream and UM – unmodified, with sample sizes shown in brackets. Asterisks indicate significant differences obtained from Kruskal-Wallis tests ($P < 0.001$ ***, < 0.01 **, < 0.05 *). Numbers sharing the same superscript are not significantly different ($P > 0.05$).

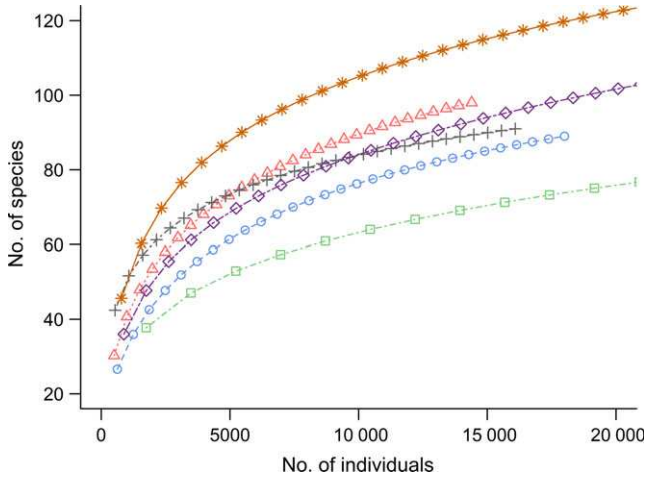


Fig. 3 Species accumulation curves based on number of sampled individuals per habitat; vegetated (green open squares), upstream (blue open circles), downstream (red open triangles), unmodified (black crosses), beaver-modified habitats combined (purple diamonds) and all habitats combined (orange stars). 95% confidence intervals are not shown for clarity but ranged from ±1.8 to ±2.7 species.

similarly effective. Unmodified habitats contained the highest proportion of unique species (38.6%), followed by vegetated (22.8%), upstream (21.0%) and downstream (14.0%) habitats. Most notably, due to a combination of variable accumulation rates, plus large differences in richness and abundance between habitats and the presence of unique taxa in each habitat, a composite sample from the four habitats resulted in greater landscape-scale richness of macroinvertebrates (mean = 28%) than for a similar sized sample of any beaver-influenced or non-influenced habitats considered independently (Fig. 3). For example, a random sample of 10 000 individuals from a landscape including both beaver modified and unmodified habitats would be expected to support 105 ± 4 species compared to 84 ± 2 species in a landscape containing no beaver-modified habitats.

Species composition

The most frequently occurring taxa were Chironomidae (present in 98% of samples), *Asellus aquaticus* (Asellidae: 90%), Oligochaeta (81%) and *Crangonyx pseudogracilis* (Crangonyctidae: 71%), with *A. aquaticus* (27.6%), *C. pseudogracilis* (19.3%) and Chironomidae (14.2%) contributing most individuals, all organisms typical of organically enriched conditions. The fauna of unmodified sites was compositionally distinct from beaver-influenced habitats (Fig. 4a). There was considerable overlap in species composition between different beaver-generated habitats that largely reflected their relative proximity: for example, macroinvertebrates of vegetated habitats were most similar to upstream habitats. The composition of upstream and downstream habitats also overlapped considerably as well as sharing part of their composition with unmodified sites. A mean BCI across all habitats of 0.61 ± 0.002 (±SE) (range: 0.15–1.00) indicated that, on average, ~39% of the overall taxon assemblage was shared between samples. Both the season sampled ($F = 3.9$, $R^2 = 0.06$, $P = 0.001$) and distance to the closest upstream sample ($F = 2.7$, $R^2 = 0.02$, $P = 0.007$; Fig. S2) had significant effects on species composition, but these were of secondary importance compared to habitat ($F = 11.8$, $R^2 = 0.25$, $P = 0.001$), with clear grouping of samples by habitat type (Fig. 4a).

Indicator taxa were mostly associated with unmodified and vegetated habitats, reflecting the strong contrast between lotic and lentic habitat (Fig. 4b). Characteristically, limnophilic species within the Dytiscidae, Heteroptera and Gastropoda (e.g. *Radix balthica*: Lymnaeidae) were associated with vegetated habitats, together with larval insects noted for their tolerance of anoxia (e.g. *Cloeon dipterum*: Baetidae). By contrast, rheophilic taxa, such as members of the Leuctridae, Baetidae (*Baetis rhodani*), Heptageniidae (*Rithrogena semicolorata*) and Elmidae, and the free-living caddis (e.g. *Rhyacophila dorsalis*), were associated with unmodified habitats.

Functional feeding group composition

The percentage of individuals within each functional feeding group varied across habitats (all tests; $\chi^2_3 > 9.5$, $P < 0.023$; Fig. 5). Filter feeders were most characteristic of unmodified habitats, while shredders, and to a lesser extent collector-gatherers, dominated beaver-modified habitats. Variations in predator abundance were low between all habitats. Significant seasonal differences in feeding group abundance did occur within habitats (Table S3), but were of minor importance compared to the differences between habitats.

Discussion

Changes in habitat and physicochemistry due to dam building

Small, straightened and unnaturally uniform streams are ubiquitous in anthropogenically modified landscapes. A lack of variation in depth, substratum and velocity, and poor lateral connectivity may have catchment-wide implications, including reduced biodiversity, low nutrient retention and poor flood attenuation. At our study

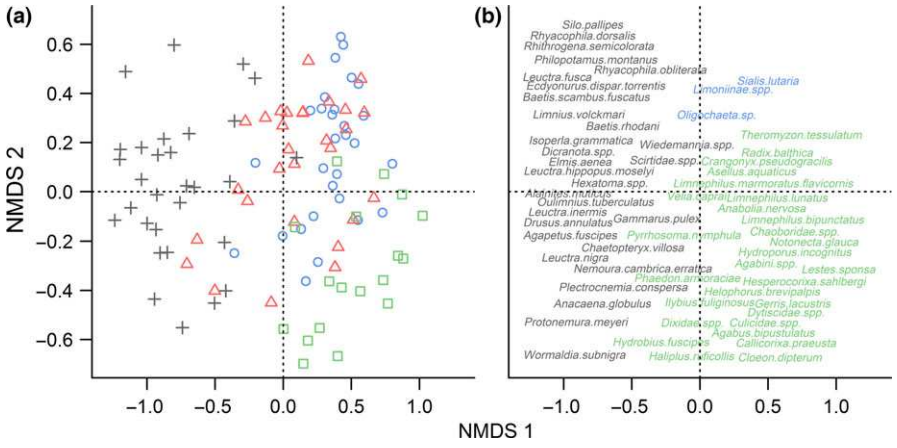


Fig. 4 Non-metric multidimensional scaling ordination (NMDS) of macroinvertebrate composition (a) based on a Bray–Curtis dissimilarity matrix per habitat; vegetated (green, open squares), upstream (blue, open circles), downstream (red, open triangles) and unmodified (black, crosses). All stress values were <0.12. Indicator species significantly associated each habitat ($P < 0.05$) are shown in plot (b).

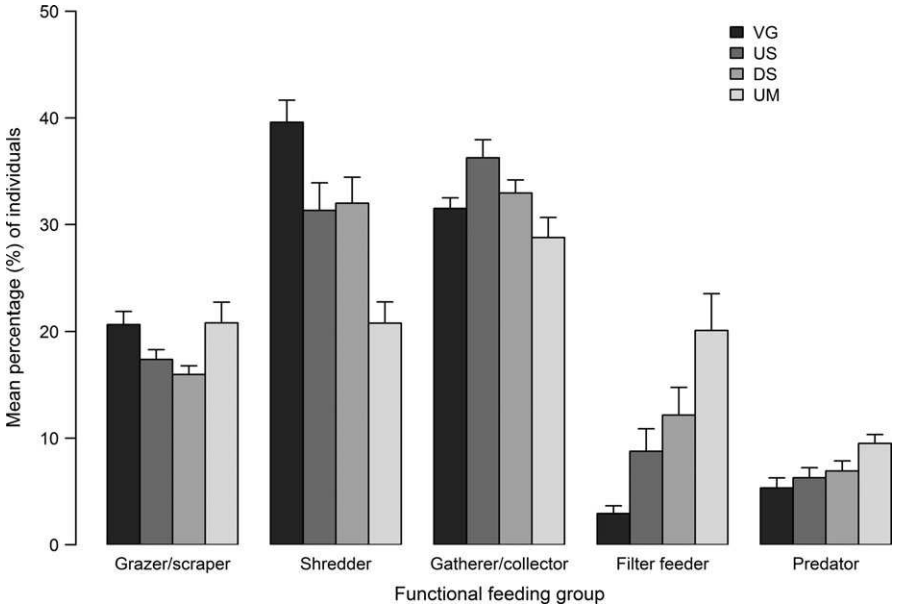


Fig. 5 The mean percentage of individuals in each functional feeding group per habitat. Error bars indicate standard error. VG, vegetation; US, upstream; DS, downstream; UM, unmodified.

site, the reintroduction of beavers initiated several years of habitat engineering that served to re-establish physical heterogeneity by creating a network of ponds, woody debris caches and aquatic plant-rich habitats, interspersed with running water.

The attenuation of peak flow is a common phenomenon in beaver-influenced streams, especially where dams occur at high density (Rosell *et al.*, 2005; Nyssen, Pontzeele & Billi, 2011), and is consistent with our observations of reduced variation in stage below a series of dams. The accumulation of fine sediment and organic matter behind beaver dams is closely linked to the reduction in downstream transport and the increased input of felled or dead wood to the channel (Gurnell, 1998). Reported changes in stream or groundwater chemistry below beaver impoundments range from decreases (Correll, Jordan & Weller, 2000; Margolis, Castro & Raesly, 2001b) to increases (Klotz, 1998; Fuller & Peckarsky, 2011) in different fractions of N and P, and are typically related to increased hyporheic exchange due to longer channel residence times (Lautz, Siegel & Bauer, 2006). The reductions in N and P in our study are more substantial than often reported, but were only significant in the summer, consistent with reports by Margolis *et al.* (2001b) and Klotz (2010). This suggests that biological processes, such as dentrification, or assimilation by macrophytes, are mainly responsible for the observed reductions. Nutrient storage by macrophytes in impounded agricultural streams may be promoted by the lower tree shading and higher fertility than in forested streams. The 20% reduction in summer chloride concentrations that we observed below the series of dams suggests that groundwater dilution might have also played a part in the lowered nutrient concentrations, though the reduction in chloride was much smaller than that observed for P and N (49% and 43% respectively). Whether such groundwater inputs reflect the influence of dams is unknown, but

would be consistent with reports of increased sub-surface flows or baseflow associated with beaver dams (Gurnell, 1998).

It is clear that habitat engineering by beaver could promote key regulating ecosystem services in agricultural streams, such as fine sediment trapping, nutrient assimilation and flow attenuation. In such streams, these processes will normally be compromised due to channel realignment and the removal of natural features that aid retention, such as woody debris dams. However, positive effects of beaver dams on ecosystem processes at a local scale are likely to be transient, since dams are dynamic on annual to decadal time scales and may also breach during high flows (Butler & Malanson, 2005). Stability of dams in agricultural landscapes might be lower due to more variable run-off, loss of volume due to increased sediment loading or, in some cases, deliberate removal. In this study, suspended solids and dissolved organic carbon (inferred from colour) both increased downstream. The increased suspended solids probably reflect bankside burrowing, the use of poorly consolidated materials in dam construction and exposure of steep sparsely vegetated banks or accumulated fine sediment under low flows. Turbidity is normally reported to decrease below beaver impoundments, although there are exceptions (Fracz & Chow-Fraser, 2013). The observed rise in colour is most likely a consequence of the decomposition of retained wood and litter inputs, plus inundation of herbaceous vegetation and organic-rich soils, and will be favoured by longer residence time and higher temperatures during the summer. Similar rises in DOC associated with beaver activity are often reported from non-agricultural landscapes (e.g. Cirmo & Driscoll, 1993; Margolis *et al.*, 2001b).

Macroinvertebrate response to habitat engineering

Invertebrate richness varied seasonally between- and within-habitats, but in general, unmodified habitats had highest species richness. However, the response of macroinvertebrates to habitat engineering by beaver is not consistent across the literature. In South America, where *Castor canadensis* is invasive, beaver ponds also had lower invertebrate richness than unmodified sites (Anderson & Rosemond, 2007), while in North America and Northern Europe, richness either did not differ (McDowell & Naiman, 1986; Redin & Sjöberg, 2013) or was reduced relative to unmodified sites (Smith *et al.*, 1991). Differences in scale of focus (i.e. patch versus landscape) and analytical approach (e.g. taxonomic resolution or correction for sampling effort) are likely explanations for the variation in reported effects. As the number of invertebrates commonly varies strongly between samples, and richness generally reflects this differential sampling effort, invertebrate richness should strictly be estimated using individual-based rather than sample-based rarefaction.

In our study, habitat-specific accumulation curves confirmed that the vegetated and upstream habitats associated with beaver ponds accumulated species at a lower rate than downstream and unmodified habitats. This may reflect homogenisation of habitat due to retention of organic-rich sediment. Disturbance by beaver during foraging or dam maintenance could also favour habitat generalists, such as Chironomidae and *A. aquaticus* that consistently dominated vegetated samples, although Hood & Larson (2014b) suggest that active maintenance of aquatic habitat by beaver increases local niche diversity. Viewed at the landscape scale (i.e. across all habitats), invertebrate richness increased by an estimated 28% in the presence of beaver. This finding reflects sufficient turnover in species between habitats to promote coexistence at the larger scale (Harthun, 1999; Anderson & Rosemond, 2007). The benefits to biodiversity of beaver-engineered patches within a landscape have been observed in multiple groups including amphibians (Cunningham, Calhoun & Glanz, 2007), fish (Schlosser & Kallemeyn, 2000) and terrestrial plants (Wright *et al.*, 2002), although it is only in the latter case that the scale of this benefit has also been fully quantified (estimated to be a 33% increase in plant richness). The characteristics of the landscape in which effects occur should also be taken into account; in landscapes already rich in lentic habitats, the effects of beaver-created habitat on richness may be less significant, while if beaver-created habitats fully dominate the landscape, there may be a negative effect on richness due to loss of lotic habitat (Wright *et al.*, 2002). However, such concerns are probably redundant in landscapes heavily exploited by humans, as it is highly unlikely that beaver-modified habitats would dominate. Therefore, any contribution to habitat heterogeneity will be beneficial.

Changes in physical habitat structure and hydrology generated by beaver dams were related to differences in macroinvertebrate composition. Species of well-aerated flowing water and low rates of siltation, such as the caddisfly *Silo pallipes* (Goeridae), were replaced by others such as the baetid mayfly *C. dipterum* (Ephemeroptera) more typical of still waters. Species replacement in beaver-impounded areas is commonly reported (Margolis *et al.*, 2001a), but the identities of the major colonists vary and cannot be generalised at a coarse taxonomic

resolution. In our study, the generalist amphipod crustacean Gammarus pulex (Gammaridae) was present in low numbers across all habitats compared to the non-native C. pseudogracilis, which prefers littoral habitats with soft sediments (Mayer, Maas & Waloszek, 2012), and hence was more frequent and abundant in beaver-influenced sites. One possibility is that distribution patterns were influenced by interspecific competition and that increased habitat diversity favours coexistence through partitioning.

All habitats contained some unique taxa that were not simply a subset of generalists from unmodified habitats, a pattern reinforced by the similar rarity scores in all habitats. However, overlaps in composition were common, principally between upstream and downstream habitats, reflecting the broad ecological tolerance of the commoner fauna of degraded streams, plus downstream drift maintained by water flow over, around and through dams. Flow below dams created hydrologically similar conditions to unmodified sites, and therefore downstream sites were biologically and physically intermediate between the more extreme unmodified and vegetated habitats. Position of dams within a catchment has previously been reported to affect invertebrate richness and abundance, as sites situated lower down the catchment may receive greater invertebrate and organic drift (Redin & Sjöberg, 2013), or benefit from trapping of sediment or agricultural pollutants upstream (Clifford *et al.*, 1993). The number of individual macroinvertebrates was generally highest in summer in beaver-modified habitats in this and other studies (McDowell & Naiman, 1986; Smith *et al.*, 1991), reflecting the greater relative importance of non-insect taxa and the concentrating effects of low flows (McDowell & Naiman, 1986). It should be noted that as samples were taken from habitats within the same stream system the possible effect of invertebrate drift may violate statistical independence of samples, especially for the most downstream dams. However, when distance to furthest upstream sample was included in richness and composition models, it was either not significant or had a low explanatory power. Furthermore, in the NMDS analysis, no samples in close hydrological proximity were clustered together, reflecting underlying differences in species composition and confirming the importance of local habitat conditions relative to downstream drift.

Despite a long history of alteration of the drainage network and a comparative scarcity of mature ponds in the region to furnish suitable colonists, habitat engineering by beavers evidently had profound effects on macroinvertebrate assemblages in a short period of time. Artificially created ponds typically reach colonisation saturation within 3–4 years (Williams, Whitfield & Biggs, 2008); so, the beaver ponds in our study most likely contained a mature macroinvertebrate assemblage as all but one were a minimum of 4 years old at the time of sampling. Even the one dam constructed during 2011 did not have significantly lower faunal richness, implying that colonisation was rapid. It is highly likely that the proximity of beaver ponds of different ages and their hydrological connectedness aids colonisation of newly engineered ponds.

Changes in community composition were reflected in shifts in functional feeding group structure. Unmodified sites were most often characterised, in this and other studies, by an abundance of filter feeders, grazer/scrapers and scarcity of shredders (McDowell & Naiman, 1986; Margolis *et al.*, 2001a). By contrast, downstream, upstream and vegetated habitats were dominated by shredders and gatherer/collectors, which presumably profit from entrapment of particulate organic matter, plant tissue and detritus (Naiman *et al.*, 1988; Simanonok *et al.*, 2011). Accumulation and processing of organic matter and its potential downstream drift may benefit filter feeders both upstream (Nummi, 1989; Rolauffs *et al.*, 2001), and downstream (Margolis *et al.*, 2001a; Redin & Sjöberg, 2013). Emerging aquatic insects also act as conduits of material, energy and nutrients to terrestrial ecosystems with the potential to alter the dynamics of terrestrial trophic interactions (Knight *et al.*, 2005). Changes imposed by habitat engineering may therefore have wider ecological significance. Higher organisms such as bats and salmonid fish may benefit from the increased density of aerial or aquatic invertebrates (Nummi *et al.*, 2011; Kemp *et al.*, 2011), while the seasonal differences in macroinvertebrate abundance between habitats may reduce fluctuations in prey availability at coarser spatial scales.

Role of habitat engineering by beavers in the restoration of agricultural streams

Thousands of kilometres of straightened and homogenised agricultural streams overlap the native range of Eurasian and North American beavers. The potential for improving poorly retentive streams such as these through the re-establishment of small-scale natural discontinuities has been a driving force behind the reintroduction of beaver to many parts of their range (Pollock *et al.*, 2014). We illustrate that the discontinuities created by beaver through dam building are hotspots of habitat heterogeneity that promote aspects of ecosystem

processes such as retention of water, nutrients and organic matter (Törnblom *et al.*, 2011), as well as enhancing aquatic biodiversity. Admittedly, in the absence of pre-damming data on stage regime, chemistry and macroinvertebrates, the differences between habitats cannot be attributed unequivocally to beaver dams, but there is no other simple explanation for such large differences on this scale and the habitats that we studied only existed as a product of dam building by beaver.

At the landscape scale, we found that invertebrate richness, abundance and diversity were positively affected by this habitat engineering. These biological changes occurred despite the low connectivity with suitable sources of colonists within this agricultural landscape, which may have limited their dispersal. Since the vast majority of stream restoration projects rarely demonstrate a biodiversity recovery post-hydrogeomorphic adjustment (Palmer *et al.*, 2014), habitat engineering via beaver reintroductions may be especially valuable because of the apparently predictable and consistent response of a wide range of aquatic biota. Beaver modifications are local features that affect habitat heterogeneity at a coarser scale; whether such benefits remain meaningful at the catchment scale is still unclear. Nevertheless, our findings demonstrate positive ecological effects of engineering by beaver within degraded freshwater systems, arising from the construction of natural features that may prove difficult to replicate by conventional methods of habitat creation. This suggests that beaver could contribute more widely in the future to the restoration of freshwater habitats provided that suitable strategies can be adopted to support coexistence with humans.

Acknowledgments

We thank Paul Ramsay for his enthusiasm and access to the study site, those who assisted in sampling, to Garth Foster for his assistance in beetle identification and Charles Perfect for comments on the manuscript. Comments from two reviewers significantly improved this paper. This research was supported financially by the University of Stirling.

References

Anderson C.B. & Rosemond A.D. (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, **154**, 141–153.

Anderson C.B., Vanessa Lencinas M., Wallem P.K., Valenzuela A.E.J., Simanonok M.P. & Martínez Pastur G. (2014) Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. *Diversity and Distributions*, **20**, 214–222.

Benke A.C. & Wallace J.B. (2003) Influence of wood on invertebrate communities in streams and rivers. In: *The Ecology and Management of Wood in World Rivers* (Eds S. V. Gregory, K.L. Boyer & A.M. Gurnell), pp. 149–177. American Fisheries Society 37, Bethesda.

Burchsted D., Daniels M., Thorson R. & Vokoun J. (2010) The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience*, **60**, 908–922.

Butler D.R. & Malanson G.P. (2005) The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology*, **71**, 48–60.

Byers J.E., Cuddington K., Jones C.G., Talley T.S., Hastings A., Lambrinos J.G., *et al.* (2006) Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution*, **21**, 493–500.

Chao A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, **43**, 783–791.

Cirmo C.P. & Driscoll C.T. (1993) Beaver pond biogeochemistry – acid neutralizing capacity generation in a headwater wetland. *Wetlands*, **13**, 277–292.

Clifford H.F., Wiley G.M. & Casey R.J. (1993) Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology*, **71**, 1439–1447.

Colwell R.K., Mao C.X. & Chang J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.

Correll D.L., Jordan T.E. & Weller D.E. (2000) Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry*, **49**, 217–239.

Cunningham J.M., Calhoun A.J.K. & Glanz W.E. (2007) Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. *The Journal of Wildlife Management*, **71**, 2517–2526.

Dalbeck L., Luscher B. & Ohlhoff D. (2007) Beaver ponds as habitat of amphibian communities in a central European highland. *Amphibia-Reptilia*, **28**, 493–501.

Dufrêne M. & Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Elmeros M., Madsen A.B. & Berthelsen J.P. (2003) Monitoring of reintroduced beavers (*Castor fiber*) in Denmark. *Lutra*, **46**, 153–162.

Fracz A. & Chow-Fraser P. (2013) Changes in water chemistry associated with beaver-impounded coastal marshes of eastern Georgian Bay. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 834–840.

France R.L. (1997) The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. *Canadian Journal of Zoology*, **75**, 1009–1013.

Fuller M.R. & Peckarsky B.L. (2011) Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia*, **668**, 35–48.

Gibson P.P. & Olden J.D. (2014) Ecology, management, and conservation implications of North American beaver (*Castor canadensis*) in dryland streams. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 391–409.

Goslee S.C. & Urban D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.

Gurnell A.M. (1998) The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, **22**, 167–189.

Gurnell A.M., Piegay H. & Swanson F.J. (2002) Large wood and fluvial processes. *Freshwater Biology*, **47**, 601–619.

Halley D., Rosell F. & Saveljev A. (2012) Population and distribution of Eurasian beaver (*Castor fiber*). *Baltic Forestry*, **18**, 168–175.

Harthun M. (1999) The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (odonata, mollusca, trichoptera, ephemeroptera, diptera) of brooks in Hesse (Germany). *Limnologica*, **29**, 449–464.

Hood G.A. & Larson D.G. (2014a) Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. *Wetlands*, **34**, 19–29.

Hood G.A. & Larson D.G. (2014b) Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology*, **60**, 198–208.

Jones C.G., Lawton J.H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Kemp P.S., Worthington T.A., Langford T.E.L., Tree A.R.J. & Gaywood M.J. (2011) Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries*, **13**, 158–181.

Klotz R.L. (1998) Influence of beaver ponds on the phosphorus concentration of stream water. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1228–1235.

Klotz R.L. (2010) Reduction of high nitrate concentrations in a Central New York State stream impounded by beaver. *Northeastern Naturalist*, **17**, 349–356.

Knight T.M., McCoy M.W., Chase J.M., McCoy K.A. & Holt R.D. (2005) Trophic cascades across ecosystems. *Nature*, **437**, 880–883.

Lautz L.K., Siegel D.I. & Bauer R.L. (2006) Impact of debris dams on hyporheic interaction along a semi-arid stream. *Hydrological Processes*, **20**, 183–196.

Margolis B.E., Castro M.S. & Raesly R.L. (2001b) The impact of beaver impoundments on the water chemistry of two Appalachian streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2271–2283.

Margolis B.E., Raesly R.L. & Shumway D.L. (2001a) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands*, **21**, 554–563.

Mayer G., Maas A. & Waloszek D. (2012) Mouthpart morphology of three sympatric native and nonnative gammaridean species: *Gammarus pulex*, *G. fossarum*, and *Echinogammarus berilloni* (Crustacea: Amphipoda). *International Journal of Zoology*, Article ID 493420, 1–23.

McDowell D.M. & Naiman R.J. (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, **68**, 481–489.

McMaster R.T. & McMaster N.D. (2001) Composition, structure, and dynamics of vegetation in fifteen beaver-impacted wetlands in western Massachusetts. *Rhodora*, **103**, 293–320.

Meteorological Office UK (2013) Met office Ardtalnaig averages (1981–2010). http://www.metoffice.gov.uk/climate/uk/averages/19812010/sites/ardtalnaig.html. Accessed 03/04/13

Moog O. (1995) *Fauna Aquatica Austriaca*. Wasserwirtschaftskataster, Bundesministerium für Land-und Forstwirtschaft, Wien.

Morales M. & Murdoch D. (2011) *sciplot: Scientific Graphing Functions for Factorial Designs*. R package version 1.0-9. Available at: http://CRAN.R-project.org/package=sciplot.

Murphy J. & Riley J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31–36.

Naiman R.J., Johnston C.A. & Kelley J.C. (1988) Alteration of North American streams by beaver. *BioScience*, **38**, 753–762.

Naiman R.J. & Rogers K.H. (1997) Large animals and system level characteristics in river corridors. *BioScience*, **47**, 521–529.

NBN (2014) *National Biodiversity Network*. Biological Records Centre, CEH, Wallingford. http://www.nbn.org.uk/. Accessed 25/04/14.

Nolet B.A. & Rosell F. (1998) Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biological Conservation*, **83**, 165–173.

Nummi P. (1989) Simulated effects of the beaver on vegetation, invertebrates and ducks. *Annales Zoologici Fennici*, **26**, 43–52.

Nummi P. & Holopainen S. (2014) Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 326–633.

Nummi P., Kattainen S., Ulander P. & Hahtola A. (2011) Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation*, **20**, 851–859.

Nyssen J., Pontzeele J. & Billi P. (2011) Effect of beaver dams on the hydrology of small mountain streams: example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. *Journal of Hydrology*, **402**, 92–102.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B. *et al.* (2013) *vegan: Community Ecology*

Package. R package version 2.0-9. Available at: http://CRAN.R-project.org/package=vegan.

Pace M.L. & Cole J.J. (2002) Synchronous variation of dissolved organic carbon and color in lakes. *Limnology & Oceanography*, **47**, 333–342.

Palmer M.A., Hondula K.L. & Koch B.J. (2014) Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 247–269.

Pollock M.M., Beechie T.J., Wheaton J.M., Jordan C.E., Bouwes N., Weber N. *et al.* (2014) Using beaver dams to restore incised stream ecosystems. *BioScience*, **64**, 279–290.

Poole G.C. (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology*, **47**, 641–660.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. http://www.R-project.org/.

Redin A. & Sjöberg G. (2013) Effects of beaver dams on invertebrate drift in forest streams. *Šumarski List*, **11–12**, 597–607.

Roberts D.W. (2010) *labdsv: Ordination and Multivariate Analysis for Ecology*. http://CRAN.R-project.org/package=-labdsv. R package version 1.4-1.

Rolauffs P., Hering D. & Lohse S. (2001) Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia*, **459**, 201–212.

Rosell F., Bozser O., Collen P. & Parker H. (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, **35**, 248–276.

Schlosser I.J. & Kallemeyn L.W. (2000) Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, **81**, 1371.

Schmidt-Kloiber A. & Hering D. (2015) www.freshwaterecology.info – an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, **53**, 271–282. doi:10.1016/j.ecolind.2015.02.007.

Siemer W.F., Jonker S.A., Decker D.J. & Organ J.F. (2013) Toward an understanding of beaver management as human and beaver densities increase. *Human-Wildlife Interactions*, **7**, 114–131.

Simanonok M.P., Anderson C.B., Martínez Pastur G., Lencinas M.V. & Kennedy J.H. (2011) A comparison of impacts from silviculture practices and North American beaver invasion on stream benthic macroinvertebrate community structure and function in *Nothofagus* forests of Tierra del Fuego. *Forest Ecology and Management*, **262**, 263–269.

Sjöberg G. & Ball J.P. (2011) *Restoring the European Beaver: 50 Years of Experience*. Pensoft, Sofia.

Smith J.M. & Mather M.E. (2013) Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology*, **58**, 1523–1538.

Smith M.E., Driscoll C.T., Wyskowski B.J., Brooks C.M. & Cosentini C.C. (1991) Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology*, **69**, 55–61.

Sprules W.M. (1941) The effect of a beaver dam on the insect fauna of a trout stream. *Transactions of the American Fisheries Society*, **70**, 236–248.

Törnblom J., Angelstam P., Hartman G., Henrikson L. & Sjöberg G. (2011) Toward a research agenda for water policy implementation: knowledge about beaver (*Castor fiber*) as a tool for water management with a catchment perspective. *Baltic Forestry*, **17**, 154–161.

Vavrek M.J. (2011) *fossil: Palaeoecological and Palaeogeographical Analysis Tools*. http://palaeo-electronica.org/2011_1/238/index.html. R package version 0.3.0.

Wickham H. (2011) The split-apply-combine strategy for data analysis. *Journal of Statistical Software*, **40**, 1–29.

Willby N. J., Law A., Foster G. N., Ecke F. & Levanoni O. (2016) Engineering biodiversity: beavers modify macrophyte and beetle richness and diversity at multiple spatial scales (under review).

Williams P., Whitfield M. & Biggs J. (2008) How can we make new ponds biodiverse? A case study monitored over 7 years. *Hydrobiologia*, **597**, 137–148.

Wright J.P., Jones C.G. & Flecker A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Zavyalov N.A. (2014) Beavers (*Castor fiber* and *Castor canadensis*), the founders of habitats and phytophages. *Biology Bulletin Reviews*, **4**, 157–180.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of macroinvertebrate species.

Table S2. Summary of macroinvertebrate data by habitat and season (mean ± SE).

Table S3. Summary of the percentage of individuals in each functional feeding group per habitat and season.

Figure S1. Species accumulation curves based on number of sampled individuals for spring, summer and autumn, per habitat and all habitats combined.

Figure S2. Non-metric multidimensional scaling ordination of macroinvertebrate composition based on a Bray–Curtis dissimilarity matrix for the distance to closest upstream sample and per season.

(Manuscript accepted 5 January 2016)

Oecologia (2007) 152:739–750
DOI 10.1007/s00442-007-0689-z

COMMUNITY ECOLOGY

Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function

Daniel J. Manier · N. Thompson Hobbs

Received: 12 July 2006 / Accepted: 4 February 2007 / Published online: 21 March 2007
© Springer-Verlag 2007

Abstract Improving understanding of the connections between vegetation, herbivory, and ecosystem function offers a fundamental challenge in contemporary terrestrial ecology. Using exclosures constructed during the late 1950s, we examined effects of grazing by wild and domestic herbivores on plant community structure, aboveground herbaceous primary production, and nutrient cycling at six sites in semi-arid, sagebrush rangelands during 2001–2002 in Colorado, USA. Enclosures provided three treatments: no grazing, grazing by wild ungulates only, and grazing by wild and domestic ungulates. Excluding all grazing caused an increase in shrub cover ($F = 4.97$, $P = 0.033$) and decrease in bare ground ($F = 4.74$, $P = 0.037$), but also a decrease in plant species richness ($F = 6.19$, $P = 0.018$) and plant diversity ($F = 7.93$, $P = 0.008$). Effects of wild ungulate grazing on plant cover and diversity were intermediate to the effects of combined domestic and wild grazing. Aboveground net primary production was higher in both grazed treatments than in the ungrazed one ($F_{\text{wild + domestic}} = 2.98$, $P = 0.0936$ and $F_{\text{wild only}} = 3.55$, $P = 0.0684$). We were unable to detect significant effects of grazing on other ecosystem states and processes including C:N ratios of standing crops, N mineralization potential, or nitrification potential. Best approximating models revealed positive correlation between N availability and herbaceous cover and a negative correlation between herbaceous primary production and the ratio of shrub–herb cover and plant diversity. We conclude that ungulate herbivory, including both wild and domestic ungulates, had significant effects on plant community structure and ecosystem function during this 42-year span. Responses to the wild ungulate treatment were consistently intermediate to responses to the no grazing and wild + domestic grazing treatments. However, we were unable to detect statistical difference between effects of wild ungulates alone and wild ungulates in combination with livestock.

Keywords Ecosystem function · Herbivory · Semi-arid shrubland · Cover · Diversity

Communicated by Jim Ehleringer.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0689-z) contains supplementary material, which is available to authorized users.

D. J. Manier · N. T. Hobbs
Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins,
CO 80523-1499, USA

D. J. Manier (✉) · N. T. Hobbs
Forest, Rangeland and Watershed Stewardship Department,
Colorado State University, Fort Collins, CO 80523, USA
e-mail: Daniel.Manier@ColoState.edu

D. J. Manier
National Park Service, Rocky Mountain Network,
1201 Oakridge Drive, Fort Collins, CO 80525, USA

Introduction

During the last century, arid and semiarid rangelands throughout western North America have been grazed by populations of wild and domestic ungulates—most notably bison (*Bison bison*), pronghorn (*Antilocapra americana*), elk (*Cervus elaphus* Canadensis), mule deer (*Odocoileus hemionus*), domestic sheep (*Ovis ovis*) and cattle (*Bos tarus*). Ungulate herbivory influences the composition of arid and semi-arid land plant communities (see reviews of Milchunas and Lauenroth 1993;

Jones 2000), shapes their disturbance regimes (Madany and West 1983; Zimmerman and Neuenschwander 1984), and modifies the flow of energy and cycling of nutrients between producers and consumers (Coughenour 1991; Frank and McNaughton 1993; Milchunas and Lauenroth 1993; Frank et al. 1994; Hobbs 1996; Hobbs et al. 1996; Frank 1998; Lecain et al. 2000). Ungulates affect plant communities by selectively removing biomass, by physical disturbance, and by excreting nutrients in dung and urine (Hobbs 2006). Better understanding of the relationship between observed patterns in vegetation and biogeochemical processes offers a fundamental challenge in contemporary ecology. These relationships have important implications for ecosystem modeling, herbivore management, and sustaining ecosystem health and services.

Livestock are relatively recent additions to the rangelands of western North America, but their wild ungulate counterparts have an enduring co-evolution with the plant communities of these systems (e.g., Mack and Thompson 1982). The semi-arid, Inter-Mountain Basin Montane Sagebrush Steppe [Southwest Regional Gap Analysis Project (SWREGAP 2005) http://www.earth.gis.usu.edu/swgap/; *Artemisia tridentata* ssp. *vaseyana* Shrubland Alliance] of the southern Rocky Mountain Ecoregion (Bailey et al. 1994) that we studied did not support large populations of ungulates before European settlement in the late nineteenth century. Some estimates indicate that current, wild-herbivore densities may also be far greater than historic levels (e.g. Gill et al. 1999); however, even modern estimates in these large areas are problematic (e.g., Rabe et al. 2002). Further, beginning in the late 1800s and early 1900s, domestic cattle and sheep were introduced to these landscapes, grazing many areas to degraded conditions (Mack and Thompson 1982).

It is clear that the influence of large herbivores on plant communities pivots on their evolutionary history (Mack and Thompson 1982; Milchunas and Lauenroth 1993; Augustine and McNaughton 1998), and thus, it is plausible that the effects of wild herbivores on ecosystem states and processes might diverge in fundamentally important ways from the effects of livestock. Several differences in patterns of grazing by wild and domestic herbivores could be responsible for this divergence. Domestic cattle feed predominantly on herbaceous plants while wild ungulates (mule deer, elk, and antelope) include significant quantities of woody tissue in their diets, particularly during winter (Kufeld et al. 1973; Hobbs et al. 1983; Valentine and Bartsch 1990). In addition, most populations of wild ungulates are migratory, using arid rangelands primarily during the winter and early spring when plants are dormant or newly emerged, while grazing by domestic animals occurs throughout the growing season. Further, low intensity and heterogeneous spatial distribution of grazing pressures before European settlement likely resulted in limited evolutionary pressure of herbivores on plants in the region, and as a result, many plants in the region are susceptible to replacement under intense grazing pressure (Mack and Thompson 1982). Finally, typical stocking rates of livestock potentially create rates of consumption that are much higher than removal by wild herbivores (Hobbs et al. 1996). Thus, it is reasonable to hypothesize that, the differences between wild and domestic herbivores in evolutionary history, dietary preferences, season of use, and grazing intensity should give rise to differences in the effects of these herbivores on semi-arid plant communities.

Despite a clear conceptual basis for differences in effects of wild and domestic herbivores on arid land ecosystems, empirical evidence for these differences has not emerged. Here, we examine effects of long-term exclusion of grazing by wild and domestic herbivores on plant community composition, aboveground herbaceous net primary production, and nutrient cycling. Specifically, we address two questions. How does grazing by large mammalian herbivores affect the ecological functions of sagebrush steppe ecosystems? How does the removal of livestock and wild ungulates from formerly grazed communities modify the ecosystem states and processes?

Materials and methods

Research design

We studied effects of grazing-exclusion treatments originally established by the Colorado Department of Fish and Game during the late 1940s and early 1950s (Baker 1948–1956 unpublished data; characteristics of each study site are provided in Electronic Supplement A). Two important and widespread sagebrush community types converge in Colorado. Sagebrush in the northern parks and basins is classified as the sagebrush steppe found in Idaho and eastern Oregon, whereas sagebrush in the southern and far western portions of the state are most similar to the Great Basin sagebrush type (West 1988). Based on the location of several historic grazing treatments (fenced exclosures documented by Baker 1948–1956), we selected a set of six sites of similar age (created between 1954 and 1959) and similar plot dimensions (1-ha fenced plots). These communities were split evenly between three northern sagebrush steppe sites in Middle Park (Grand county), and three Great Basin sagebrush type sites further west and south in Gunnison, Rio Blanco and San Miguel, counties (Colorado). Sites in both community types were dominated by mountain

sagebrush (*Seriphidium vasyanum* Rydberg)[1] with varying amounts of rabbitbrush (*Chrysothamnus viscidiflorus* Nuttall, and *C. depressus* Nuttall) contributing to shrub composition. On the sagebrush steppe sites we routinely found snowberry (*Symphoricarpos longiflorus* Gray, *S. rotundifolius* Gray) and winterfat (*Krascheninnikovia lanata* Pursh), which were rarer on the Great Basin sites. The perennial sub-shrub, *Leptodactylon pungens*, was as ubiquitous across sites as sagebrush. In addition to the shrub canopy, stands of pinon pine (*Pinus edulis* Engelm.) and juniper [*Juniperous osteosperma* (Torr.) Little, *J. monosperma* (Englem. Sarg.)] occupied portions of the Dry Basin and Bar D landscapes (two of the Great Basin communities) in dense woodland patches and open savanna-like distributions. Nomenclature follows the University of Colorado Museum Herbarium provided by Weber and Wittmann (Weber and Wittmann 2001).

The design included six replications of three treatments: (1) ambient grazing[2] by wildlife and livestock, (2) grazing by wildlife alone, and (3) an ungrazed reference area. Each replicate contained an area that permitted grazing by wild ungulates, but that excluded domestic ungulates. This exclosure was established with 1-m high, three-strand barbed wire fencing. Each replicate also included an area protected by 3.25-m high, 7.5 × 7.5-cm steel mesh fencing, plus a single strand of barbed wire. This exclosure prevented grazing by all ungulates. The combined grazing treatment (domestic + wild ungulates) was an unfenced, 1-ha area adjacent to the other two exclosures. Hereafter, we will refer to these plots as "no ungulates" (high fence), "wild ungulates" (low fence), and "domestic + wild ungulates" (no fence). This design was unusual in allowing replicated observations of effects of different communities of herbivores accruing over years. Our sampling of the sites extended from the year 2000 (species composition and structure) through 2002 (production and N cycling) resulting in a 40+-year treatment period. One of the replicates we studied (see Woods Gulch in electronic supplement S1) had different dimensions than the others; however, the similarities in the site design and establishment, and distribution across a subset of Colorado semi-arid sagebrush communities encouraged us to utilize the historic design.

Because the spatial distribution of our sites is based on a combination of deterministic (accessibility and target population biases of the Colorado Fish and Game) and a stochastic events (resulting in the preservation of a subset of the original sites) and not a proper spatial design, extrapolation of our results to other sagebrush communities should be made with caution. Further, the treatments may not reflect the "true" density of wild ungulates in the area because the long-term distribution of animals across these areas was not considered in the design. However, we emphasize that given the spatial and temporal heterogeneity inherent in grazing patterns by herbivores (reviewed by Augustine and McNaughton 1998; but also see Lubchenco 1978; Sommer 1999; Hillebrand 2003), this criticism can be offered for any study of grazing effects using small-scale exclosures. Despite these problems, our work offers value by integrating effects of herbivory over 40 years at replicated sites.

Measurements of plant community composition

We first (2000) sampled vegetation cover and species composition at each site using modified Whittaker plots (Stohlgren et al. 1995) during the peak of the growing season. We estimated cover in each of ten, 1-m^2 plots nested within a 1,000-m^2 plot. Each species occurring within a 1-m^2 plot was recorded along with the sum cover of that species within the plot. Plots were located inside each fenced area (no ungulates and wild ungulates) and outside, adjacent to each fenced area (wild + domestic ungulates).

Measurements of primary production and grazing intensity

We estimated primary production of biomass by herbivores using temporary, movable cages to isolate plots from herbivores (Frank and McNaughton 1992; McNaughton et al. 1996) during two consecutive growing seasons (2001 and 2002). Aboveground net primary production (ANPP) of herbaceous plants was estimated as the positive increments in plant biomass accruing under cages during 30-day intervals during the growing season (April–May, May–June, June–July intervals with sampling visits between each interval). We used a modification of the canopy intercept technique for estimating standing crop biomass inside and outside of cages on each sample date (Frank and McNaughton 1990, 1992). Ten paired open and caged plots (1 m^2) were randomly distributed across each treatment. Each point consisted of a caged 1-m^2 plot and an adjacent, open 1-m^2 plot.

Models describing the relationship between pin-hits and standing, oven-dry biomass were selected from the choice of a linear or second-order polynomial regression for each of four vegetation classes. We developed individual regressions for each of four life forms: (1) broad-leaved, caulescent grasses; (2) caespitose, bunch grasses; (3) cauline dicots; and (4) rosette or caespitose dicots (equations and statistics provided in Electronic Supplement S2).

[1] We likely encountered *Seriphidium arbusculum* on four, or more, of the sites. However, we did not distinguish this species from *S. vasyanum*, because we did not witness the phenology necessary for the distinction (Weber and Wittmann 2001).

[2] We use the term "graze" to include feeding on grasses, forbs, and shrubs.

Estimation of plant C:N ratios

We retained samples from the clipped plots for analysis, generating replicates within treatments, months, and years. We incinerated ground samples in a combustion thermoanalyzer (Leco CHN-1000; LECO Corporation, St Joseph, Mich.) to determine the organic C and N content in each plant sample. We calculated the standing crop of N as the product of the total standing crop of plant dry matter multiplied by the respective N content of each vegetation group.

Estimation of soil N potentials

Soil N mineralization and nitrification potentials were assessed using laboratory incubations of field-collected soils. We stratified samples within each treatment by associations with shrub canopies, grass patches, or bare ground interspaces creating a 3×3 factorial design using treatments and vegetation associations. We extracted soil surface samples (top 10 cm) from each of the treatments replicating associations with shrub, grass, or absence of cover. We refrigerated samples and returned them to the laboratory where they were stored briefly in an industrial freezer. Moisture content of each sample was estimated by selecting a sub-sample, weighing, oven drying and re-weighing each sample. We further divided soil cores, separating one set for immediate extraction using 75 ml of 2 M KCl–PMA, and another for incubation.

Aerobic incubations were conducted in a temperature-controlled room (20°C) for 30 days at laboratory estimated soil water field capacity (Garcia-Montiel and Binkley 1998; Rueth and Baron 2002). After incubation, the second set of samples was extracted using the same technique. NO_3 and NH_4 were measured from each extraction using an autoanalyzer (Alpkem 3500 series; Perstorp Analytical Company, Wilsonville, Ore.). Differences in N concentrations between the pre- and post-incubation soils indicated the mineralization potential (biochemical transformation from ammonium to nitrate) and potential nitrification rate (microbial generation of ammonium), which was indicative of microbial activities in the soils and nutrient availability.

Statistical analyses

The six locations were analyzed as replicates; however, the locations were distributed across a relatively broad region (from a replicate perspective) with many similarities, yet the potential for local environmental differences. Thus, we assumed that environmental differences between these semi-arid sites were minor compared to the similarities manifested as similar community composition and structure. We also considered blocking the data by vegetation type; however, preliminary analyses indicated that this offered no additional power. From a wider, biogeographic perspective, while these sites bear similarities to identified forms of sagebrush communities, they are all within western Colorado, quite similar to one another, and at the boundaries of classifications, such that they can be considered replicate samples within this transitional region.

ANOVA were conducted on arc-sine square root transformed estimates of percent cover across grazing treatments in each of three vegetation classes: grasses (and grass-likes), forbs, and shrubs. Net differences in the distribution of vegetation cover, species richness and evenness, net annual aboveground production, plant C:N contents, soil N mineralization and nitrification due to treatments were assessed by comparing net treatment effects using ANOVA ($\alpha = 0.10$). We compared effects of the treatment across the growing season by testing repeated, monthly sample intervals of production and plant C:N in a repeated measures ANOVA (RMANOVA; $\alpha = 0.10$). We used unstructured covariance in our analyses because plot locations were moved after each interval (as part of the design) protecting the independence of each sample and homogenizing variance (reduced heteroscadicity). Analysis of the soil data included statistical comparisons of grazing treatments, vegetation associations, and location (site) across the incubation period (increment) using RMANOVA ($\alpha = 0.10$); unstructured covariance structure was used because there was not an indication of patterned variance in preliminary analyses. We chose $\alpha = 0.10$ to achieve a reasonable compromise between the probability of a type I error and the power of the test in a study where our sample size was fixed by historic precedent and could not be adjusted to increase power.

Differences among treatment means were examined with a priori, single *df* contrasts. We report these contrasts, as well as confidence intervals, on effect sizes. We viewed the contrast between the wild ungulates only (low fence exclosure) and the no grazing treatment (high fence exclosure) as an estimate of the effect of grazing by wild ungulates. We viewed the contrast between the wild + domestic ungulate treatment (no fence) and the no grazing treatment (high fence) as an estimate of the combined effects of grazing by wild and domestic ungulates. We viewed the contrast between the wild ungulates only treatment (low fence) and the wild + domestic ungulates treatment (no fence) as an estimate of the additive effect of domestic ungulates on wildlife herbivory effects.

We examined the effect of plant community structure on ecosystem function by testing all possible models, without interactions, that related measured ecosystem processes (ANPP, N mineralization, nitrification, C:N accumulation) to measured states of the plant community (cover and diversity). We selected best approximating models by

comparing the Akaike weights (w_r) estimated for each model (Burnham and Anderson 1998).

Results

Effects on plant cover and diversity

The combined effects of grazing by wild and domestic ungulates changed the structure and diversity of the sagebrush steppe communities. Cover of shrubs was greater, and there was less bare ground, in the no ungulates plots than in the area grazed by wild and domestic ungulates (shrub cover, $F = 4.97$, $P = 0.0328$; bare ground $F = 4.74$, $P = 0.0366$; Table 1). The ratio of shrub cover to herbaceous cover was almost three-fold greater in the no grazing exclosures relative to the open rangeland ($F = 3.91$, $P = 0.0563$; Table 1). We could not detect effects of wild + domestic grazing on total herbaceous cover or total vegetative cover. However, confidence intervals on the effect size of combined ungulate grazing on total vegetative cover (Table 1) indicated that we could not rule out large reductions in plant cover attributable to grazing, but we could eliminate the possibility of large enhancing effects.

Species richness and evenness were lower in the no ungulates treatment relative to wild + domestic treatment (richness $F = 6.19$, $P = 0.0181$; evenness $F = 7.93$, $P = 0.0081$; Table 1). Differences in richness and Shannon–Weiner diversity between treatments were apparent in the spatial separation demonstrated in Fig. 1; these results showed consistently greater diversity with grazing disturbance.

Wild + domestic grazing had greater effects on shrub cover than grazing by wild ungulates alone ($F = 3.89$, $P = 0.0571$; Table 1). We failed to observe other significant contrasts between wild and wild + domestic grazing. However, strongly skewed confidence intervals on effect sizes suggested that increased replication could show that bare ground and evenness were greater in the combined ungulate treatment than in the wildlife only treatment. Moreover, means for the wild ungulate treatment were intermediate to the other treatments for all plant cover and diversity responses except herbaceous cover.

Effects on herbaceous production

ANPP averaged approximately 7 g/m^2 higher in the wild + domestic ungulate and the wild ungulate treatments relative to the no grazing treatment ($F_{\text{wild + domestic}} = 2.98$, $P = 0.0936$ and $F_{\text{wild only}} = 3.55$, $P = 0.0684$; Table 1; Fig. 2). The enhancing effect of grazing on ANPP was greatest at low levels of ANPP (Fig. 2). We did not detect

Table 1 Mean values by treatment and results of contrast comparisons reflecting the difference between the treatment means indicated in each column. Means for each response variable with the *same letter* are not significantly different. *ANPP* Aboveground net primary production

Response	Wild and domestic ungulates		Wild ungulates		No ungulates		Confidence intervals on effect sizes[a]		
	Mean	SEM	Mean	SEM	Mean	SEM	Wild and domestic vs. wild ungulates	Wild and domestic vs. no ungulates	Wild vs. no ungulates
Sum vegetation cover	34.54	2.15	43.71	5.89	44.37	5.44	(−20.64, 2.31)	(−21.31, 1.64)	(−12.14, 10.81)
Shrub cover	17.41 b	2.43	25.14 a	3.35	26.15 a	2.44	(−14.37, − 1.09)	(−15.38, − 2.10)	(−7.65, 5.63)
Herbaceous cover	17.13	1.05	18.57	2.86	18.22	3.20	(−7.54, 4.67)	(−7.19, 5.02)	(−5.76, 6.45)
Shrub:herbaceous	1.11 a	0.18	1.50 a,b	0.20	3.07 b	1.19	(−2.08, 1.28)	(−3.65, −0.28)	(−3.25, 0.11)
Bare ground	48.41 a	5.95	39.61 a,b	3.91	32.62 b	5.30	(−3.47, 21.06)	(3.52, 28.06)	(−5.27, 19.26)
Richness	20.83 a	0.75	19.67 a,b	0.64	17.50 b	1.31	(−1.10, 3.43)	(1.07, 5.60)	(−0.10, 4.43)
Shannon-Weiner (*H*)	2.42 a	0.07	2.21 a,b	0.08	2.00 b	0.15	(−0.04, 0.45)	(0.16, 0.66)	(−0.04, 0.45)
ANPP	36.74 a	1.97	37.33 a	2.38	30.24 b	3.41	(−6.96, 5.78)	(0.13, 12.86)	(0.72, 13.45)
Plant C:N May	21.30	0.69	20.62	0.69	21.92	0.96	(−1.19, 2.55)	(−2.49, 1.25)	(−3.21, 0.61)
Plant C:N July	33.69	1.28	31.71	1.23	34.30	1.70	(−1.42, 5.38)	(−4.02, 2.78)	(−6.00, 0.80)
Potential N mineralization (μg N/g soil)	983.04	152.90	1,213.46	124.94	1,031.29	104.99	(−539.40, 78.60)	(−357.30, 260.80)	(−126.80, 491.20)
Potential nitrification (μg N/g soil)	1,109.56	168.03	1,353.29	126.34	1,192.22	88.99	(−559.20, 71.70)	(−398.10, 232.80)	(−154.40, 476.50)

[a] Calculated based on the difference between the treatment means indicated, i.e. wild and domestic vs. wild ungulates = wild and domestic mean − wild ungulates mean

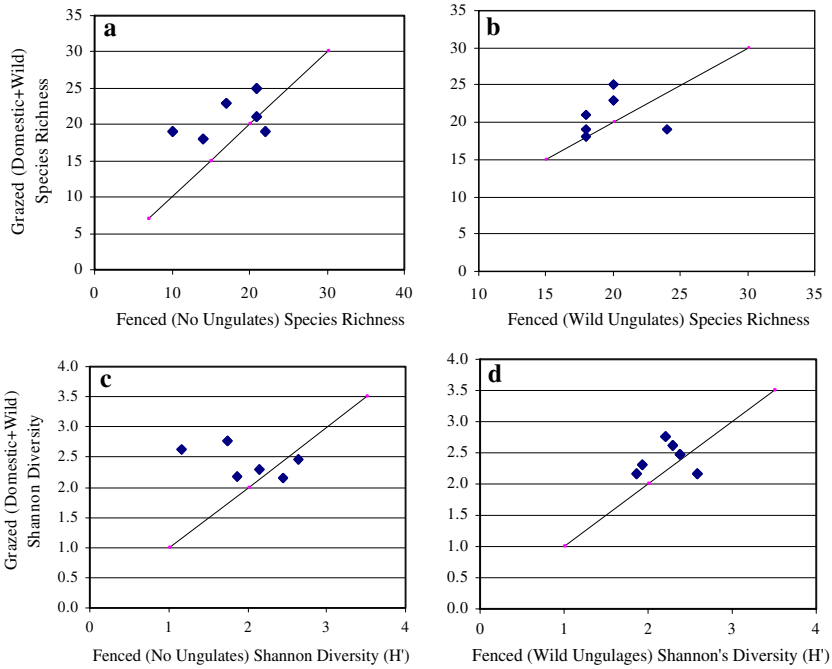


Fig. 1 Differences in richness (**a, b**) and evenness (Shannon–Wiener diversity; **c, d**) between grazing treatments. The *diagonal lines* represent unity

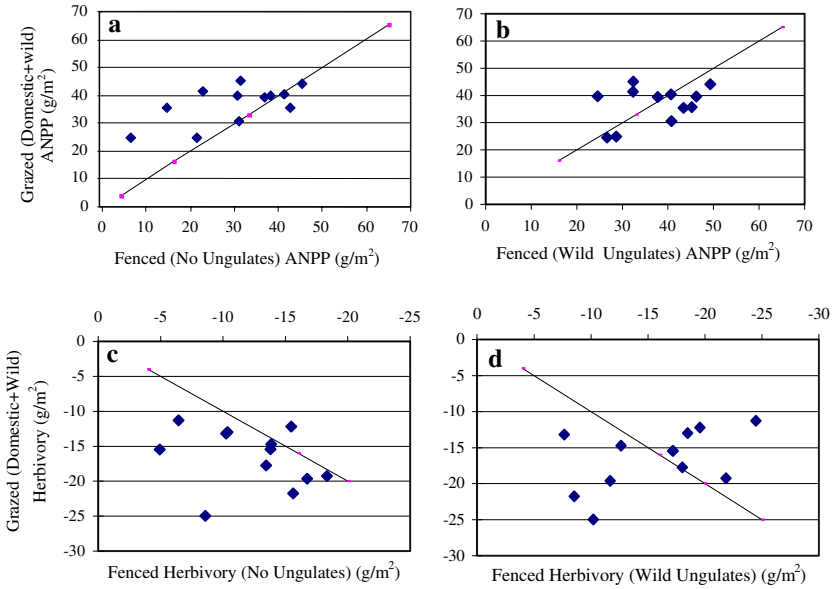


Fig. 2 The treatment effect on aboveground net primary production (*ANPP*) (**a**, **b**), and measured herbivory (removal) (**c**, **d**) for 2 years and six replicates. **a**, **c** The *x*-axis represents plots with no ungulate herbivory. **b**, **d** Plots with wild herbivores, but no cattle, along the *x*-axis. *Solid diagonal lines* represent unity

significant differences in ANPP between the wild ungulate only treatment relative to the combined grazing treatment (Table 1; Fig. 2).

Trends in soil N potential

We were unable to detect effects of grazing on potential N mineralization or nitrification (Table 1). However, we found differences in N cycling rates between different sites and local vegetation associations; differences that appeared to be related to local variation in plant cover. Mineralization and nitrification rates were lower in bare patches compared to vegetated patches (Fig. 3). Moreover, we found that the association of surface soils with vegetation was a significant predictor of the differential distribution of nitrification potential ($F = 17.97$, $P < 0.0001$) and N mineralization potential ($F = 18.05$, $P < 0.0001$; Table 2). These models also revealed significant differences in N cycling among study sites ($F_{\text{nitrification}} = 11.59$, $P < 0.0001$; $F_{\text{mineralization}} = 9.86$, $P < 0.0001$; Table 2).

Trends in plant C:N

We found no effect of treatment on C:N ratios of herbaceous plant tissue (Table 1). Means were similar and confidence intervals on effect sizes were relatively tight,

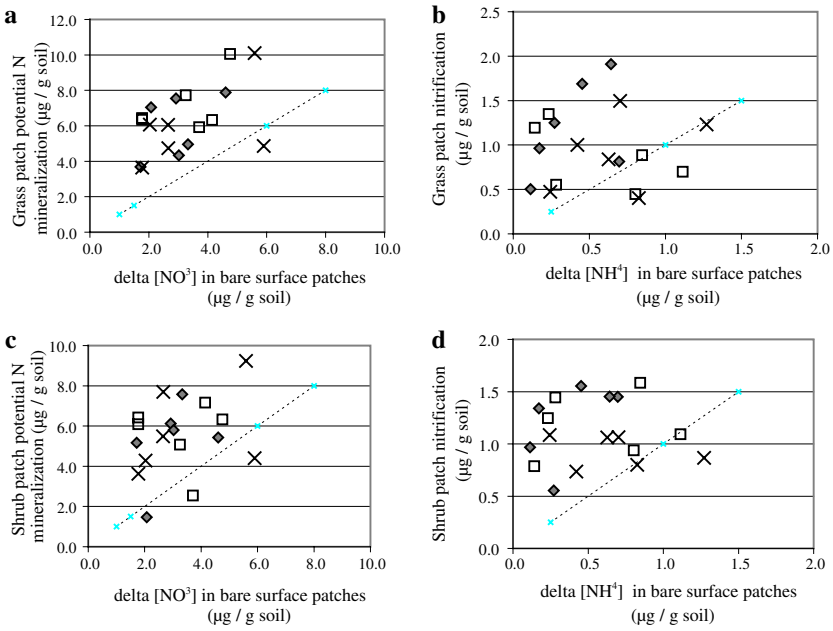


Fig. 3 Distribution of changes in NO_3 and NH_4 concentrations determined from 30-day incubation. Differences between vegetation associations are compared using the two axes. Soils from six sites are combined with separation in symbols based on grazing treatments (*solid diamonds* no ungulates, *open squares* wild ungulates only, *crosses* domestic + wild ungulates)

Table 2 Net potential nitrification and daily N mineralization from 30-day in vitro incubation at field capacity. Result of repeated measures ANOVA for within-subject effects of the hypothesis that there was no change during the incubation (*Increment*) and no difference between treatment, replicate, and vegetation association. *TRT* Grazing treatment effect, *SITE* Between-replicate effect, *VEG* effect due to association with shrub canopy, grass patch, or bare ground

Source	*df*	Type III SS	Mean square	*F*-value	Pr > *F*
Nitrification					
Increment[a]	1	0.7783	0.7783	264.23	<0.0001
Increment × TRT	2	0.0068	0.0034	1.16	0.3149
Increment × SITE	5	0.1707	0.0341	11.59	<0.0001
Increment × VEG	3	0.2680	0.0893	30.33	<0.0001
Error (Increment)	258	0.7600	0.0029		
N mineralization					
Increment	1	879.6341	879.6341	309.45	<0.0001
Increment × TRT	2	4.5892	2.2946	0.81	0.4472
Increment × SITE	5	140.2025	28.0405	9.86	<0.0001
Increment × VEG	3	247.4540	82.4847	29.02	<0.0001
Error (Increment)	258	733.3924	2.8426		

[a] Increment reflects changes over time, i.e. due to incubation

indicating that our failure to detect differences did not result from low statistical power.

Relationships between community structure and ecosystem processes

Regression modeling revealed that herbaceous primary production, N mineralization potential, and nitrification potential, were best predicted using a combination of plant cover and diversity indices as independent variables (Table 3). The most parsimonious model of primary production indicated a negative effect of the ratio of shrub:herbaceous cover, a positive effect of plant richness and a negative effect of Shannon–Weiner diversity ($W_r = 0.467$, $r^2 = 0.52$; Table 3). The best models for N mineralization and nitrification also included a combination of shrub and herbaceous cover and the two diversity measures, richness and the Shannon–Weiner index diversity ($W_r = 0.553$, $r^2 = 0.49$, and $W_r = 0.580$, $r^2 = 0.51$, respectively; Table 3). The best fitting models for both nitrification potential and N mineralization potential indicated negative effects of shrub cover, positive effects of herbaceous cover, and negative correlation with the Shannon–Weiner index. Other descriptive models indicated positive effects of plant richness on N cycling in addition to cover and diversity index correlations (Table 3).

Best approximating models of standing N in May and July (the amount of biomass, adjusted to reflect its N content) included a positive herbaceous cover effect and a negative richness effect ($r^2 = 0.87$ and $r^2 = 0.91$, respectively; Table 3). Our best multivariate models of plant C:N explained only a small portion of the variability in plant C:N, but we previously connected these processes and pools to vegetation associations so this lack of correlation was not surprising.

Discussion

This paper focuses on two questions. How does grazing by large mammalian herbivores affect the structure and function

Table 3 Selected models relating ecosystem processes to vegetation cover and diversity. *RMSE* Root mean squared error, *AIC* Akaike's information criterion, w_r weighted Akaike index, *herb.* herbaceous, *potent.* potential, *Nmin.* N mineralization

Dependent Variable	Equation	RMSE	*df*	r^2	AIC	w_r
$ANPP_{herb.}$ =	40.16 − 2.42 Shrub:herb. + 0.98 richness − 8.91 Shannon	6.90	32	0.52	142.84	0.467
$ANPP_{herb.}$ =	21.47 − 1.63 Shrub:herb. + 0.85 Shannon	7.29	33	0.45	145.87	0.102
$ANPP_{herb.}$ =	5.16 + 0.41 Herb. cover + 1.15 richness	7.31	33	0.44	146.10	0.091
Nitrification potent. =	2,148.79 − 25.12 + 44.87 Herb. cover − 525.52 Shannon	338.87	32	0.49	423.21	0.553
Nitrification potent. =	2,144.85 − 27.15 Shrub cover + 43.63 herb. cover + 13.79 richness − 613.26 Shannon	342.56	31	0.50	424.84	0.244
Nitrification potent. =	1,653.79 − 28.44 Shrub cover + 49.89 herb. cover + 34.54 shrub:herb. + 16.41 richness − 481.12 Shannon	345.50	30	0.51	426.28	0.119
Nmin. potent. =	1,991.08 − 24.80 Shrub cover + 44.55 herb. cover − 519.17 Shannon	327.70	32	0.51	420.79	0.580
Nmin. potent. =	1,990.55 − 25.08 Shrub cover + 44.38 herb. cover + 1.85 richness − 530.93 Shannon	332.91	31	0.51	422.78	0.214
Nmin. potent. =	1,504.50 − 26.36 Shrub cover + 50.58 herb. cover + 34.19 shrub:herb. + 4.44 richness − 400.14 Shannon	335.68	30	0.51	424.20	0.106
Standing N_{May} =	6.96 + 2.70 Herb. cover − 0.82 richness	9.03	31	0.87	152.51	0.295
Standing N_{May} =	−6.08 + 2.55 Herb. cover	9.28	32	0.85	153.43	0.186
Standing N_{May} =	7.94 − 0.09 Shrub cover + 2.77 herb. cover − 0.83 richness	9.15	30	0.87	154.27	0.122
Standing N_{July} =	4.70 + 1.46 Herb. cover − 0.36 richness	3.96	33	0.91	101.91	0.271
Standing N_{July} =	−1.13 + 1.40 Herb. cover	4.06	34	0.90	102.90	0.165
Standing N_{July} =	4.04 + 0.06 Shrub cover + 1.42 herb. cover − 0.35 richness	3.99	32	0.91	103.35	0.132
Plant $C:N_{May}$=	20.65 − 0.16 Herb. cover + 0.18 richness	2.39	31	0.22	62.05	0.192
Plant $C:N_{May}$=	23.56 − 0.12 Herb. cover	2.42	32	0.17	62.16	0.181
Plant $C:N_{May}$=	22.06 − 0.18 Herb. cover + 0.27 richness − 1.25 Shannon	2.39	30	0.24	63.01	0.118
Plant $C:N_{July}$=	27.37 + 2.65 Shannon	4.87	34	0.04	115.89	0.128
Plant $C:N_{July}$=	28.46 + 0.25 Richness	4.90	34	0.03	116.37	0.100
Plant $C:N_{July}$=	34.77 − 0.07 Shrub cover	4.93	34	0.02	116.79	0.081

of sagebrush steppe ecosystems? How does the addition of livestock to communities of wild ungulates modify the effects of wild species on ecosystem states and processes? We obtained a clear answer to the first question and an answer that was less clear for the second one.

Effects on community structure

Forty-two years of exclusion of grazing by wild and domestic ungulates caused fundamental shifts in the composition and diversity of sagebrush steppe plant communities. The most notable change was a threefold increase in the ratio of shrub cover to herbaceous cover in areas where grazing was excluded; based on local observations, the shrub cover within the protected areas was aberrant from the size and density of shrubs in the immediately surrounding landscape. Total vegetative cover increased inside wild ungulate + livestock exclosures relative to the open grazing treatment, but we failed to detect changes in herbaceous cover there, despite increases in the cover of shrubs. Excluding grazing by all large herbivores caused clear reductions in biological diversity as indicated by richness and evenness.

We cannot assert statistically that the effects of wild ungulate grazing were modified by the addition of livestock because confidence intervals on the effect-size of wild ungulates versus wild and domestic ungulates overlapped zero for all responses observed. However, some confidence intervals on the additive effect of livestock were strongly skewed, indicating that we cannot rule out effects that could be quite large. This was particularly true for total vegetative cover, shrub cover, Shannon–Weiner values, and potential N mineralization and nitrification. Although we could not detect differences between the wild ungulates only treatment and the other treatments, means of the wild ungulate only treatment were intermediate to the other two treatments for all metrics of community composition and diversity. This suggests that adding livestock to the native

ungulate community increased the impact of native ungulates on plant community structure.

Previous studies of grazing-exclusion effects on community structure of semi-arid rangelands in western North America have produced mixed conclusions. In contrast to our findings, Stohlgren et al. (1999) found no statistically significant differences in plant cover or species diversity due to herbivore exclusion in several Rocky Mountain grasslands. Willms et al. (2002) also found no significant differences in species diversity as a result of excluding grazing in mixed-grass prairie. These results contrast with other evidence indicating that species diversity may decline in the presence of grazing (Reynolds and Trost 1980; Chew 1982; Hillerbrand 2003). Other studies have shown similar effects of grazing on shrub cover, specifically, increased woody cover in response to grazing exclusion (Schultz and Leininger 1990; Coughenour 1991; Singer 1996). However, Singer (1995) found responses of shrubs to grazing only on low elevation sites, predominantly big sagebrush (*Seriphidium tridentatum*), but no effects on *Seriphidium vaseyanum*, typical of slightly higher elevations and deeper soils, which predominate our sites.

Our results may differ from studies that failed to find effects on plant cover and diversity because many of these studies suffered from a short duration of grazing treatments or low power when making comparisons within a vegetation type. For example, analyses of effects reported by Stohlgren et al. (1999) made comparisons across nine grassland sites, lumping plant communities across western North America. It is not surprising that, in the face of such variation, significant effects of grazing on plant communities were not detected. Ours is the first, replicated and long-term, controlled study of grazing effects within a targeted vegetation type. Additional, similar, research in other regions and vegetation types would be beneficial for comparison of long-term effects.

Effects on ecosystem states and processes

Long-term exclusion of large herbivores from sagebrush steppes appeared to cause substantial reductions in herbaceous ANPP relative to the grazed condition. Further, expansion of woody species has been shown to reduce herbaceous ANPP in mesic grasslands (Lett and Knapp 2006), and arid grasslands (Aguiar et al. 1996; Huenneke et al. 2002), resulting in a loss of ecosystem function when shrub production does not compensate for the loss in herbaceous production. The combined wild domestic and the wild ungulates only treatments showed significantly greater ANPP than the ungrazed treatment. Milchunas and Lauenroth (1993) analyzed data from arid and semi-arid rangelands around the world and found a significant influence of protection from grazing in shrub communities, and a potential for increased primary production in grazed systems compared to ungrazed systems. Positive correlation between grazing intensity and production has been observed on sagebrush steppe rangelands in Yellowstone National Park (Frank and McNaughton 1992, 1993). However, these correlations likely reflected relatively short-term effects of grazing. We are the first to show enhancing, long-term effects of grazing on herbaceous ANPP in sagebrush steppe. We surmise that at least part of these effects may have come from negative feedback of increased dominance of shrubs in the grazing-excluded treatment. Our wild ungulates only treatment had (high) shrub cover similar to ungrazed areas, but wild ungulate activities were sufficient to stimulate primary production such that ANPP was not significantly different from the open grazing treatments (Table 1). This is an additional indication of the interaction, because if primary production were only connected to competition, we would expect to find grass production inversely correlated with shrub cover (e.g., Heisler et al. 2003; Beeskow et al. 1995).

In contrast to our findings on ANPP, we failed to find any effects of grazing exclusion on other ecosystem states and processes. This failure can be attributed to replication that was inadequate to overcome variability in N cycling and availability among sites; however, we were restricted in this aspect of the design because we were using historic structures. Confidence intervals on effect sizes for N mineralization and nitrification were particularly broad.

Relationships between community structure and ecosystem processes

Our regression analysis revealed relationships between cover and diversity of sagebrush communities and ecosystem processes. Best approximating models predicting herbaceous ANPP, N mineralization and nitrification potentials, and N standing crop consistently contained independent variables indexing community composition, shrub cover, herbaceous cover, or their ratio. Increasing shrub cover and declining herbaceous cover were consistently correlated with declines in these dependent variables.

Ecosystem properties respond to the effects of herbivory by ungulates through variation in species composition of plant communities, differences in plant growth and reproductive phenologies, and variability in the affects of other disturbances, particularly fire (Hobbs 1996; Augustine and McNaughton 1998). We found that herbaceous production and N cycling in this semi-arid shrubland were negatively affected by woody cover and positively affected by herbaceous cover. Additionally, trends in cover were affected by herbivore treatments. Belsky and Blumenthal (1997) reviewed research on the effects of livestock grazing and concluded that ungulates produced a range of effects, such as reduced herbaceous cover and litter, compacted soils,

reduced water infiltration rates, and increased erosion potential. In contrast, Milchunas and Lauenroth (1993) found a significant potential for increased primary production in grazed systems compared to ungrazed systems. However, they concluded that the effects of herbivores on above- and belowground production were minimized by environmental stresses applied by regional abiotic patterns in soil and climate (Milchunas and Lauenroth 1993). Our findings provide some support for each of these views. We clearly identified differences in vegetation structure and extent of bare ground due to the grazing treatments, but we also detected enhanced ANPP in grazed areas.

The correlations between N mineralization and nitrification potentials, and the N content of the vegetation (standing N) and shrub and herbaceous cover indicate the association of herbaceous vegetation (and litter) with more rapid N cycling, and the relatively negative effect of shrub cover and litter on N cycling in this system. The fact that herbaceous cover and productivity of grazed areas remained high relative to the ungrazed one suggests that belowground processes, such as N cycling, are maintained; however, increased bare ground in grazed treatments may counteract the net benefit when budgets are calculated across a wide area.

We did not find significant differences in plant C:N between treatments. We did find changes in mean C:N over the growing season as N contents declined while grasses and herbs matured and completed reproductive cycles. Regression results indicated that vegetation cover affected spring C:N, possibly revealing an effect of greater soil N availability in the spring, or greater N concentrations in young plants. Studies which have simulated differences in herbivory frequency (clipping of vegetation) have documented significant increases in N concentrations and net N yield (standing N) with greater removal (Green and Detling 2000; Leriche et al. 2003). However, this effect is dependent on N availability. Our results did not indicate differences in plant C:N between treatments; considering that we also did not find significant differences in N cycling rates, these findings support the conclusions of Leriche et al. (2003) suggesting that N limits may supersede herbivory effects.

Interactions between vegetation and the activities of ungulates are manifested in indirect effects of the herbivores on nutrient cycling. Herbivores react to the distribution of resources (vegetation as food and protective cover) and have a direct impact on vegetation and nutrient distributions (Augustine and McNaughton 1998). Soil N cycling changes as litter quantity and quality are altered by herbivory and by the addition of readily available N to upper levels of the soil in urine and feces (Hobbs 1996, 2006). As a result, existing heterogeneity in the spatial distribution of N within landscapes is amplified by ungulate selection of habitats and patches (Hobbs 1996, 2006; Augustine et al. 2003). Therefore, as herbivores directly affect the composition and structure of the vegetation, they also affect plant–soil relationships by altering biomass and nutrient inputs. We observed differences in N cycling relative to vegetation cover, which indicated that ungulate driven shifts in cover might drive changes in ecosystem processes through shifts in the composition of vegetation. However, we did not find significant differences in herbaceous cover, potential N mineralization, or nitrification between grazing treatments. Our investigations did not preclude the alternate possibility, i.e., a previous decline or scarcity in N availability may be driving patterns in both cover and animal distributions as previously described by Hobbs (1996) and Augustine et al. (2003). Because N availability is a critical component of primary production, this remains a logical possibility. Similarities in plant C:N across treatments (Fig. 4; Table 3) indicated that the plants did not realize differences in N availability during this study. Similarly, Stark et al. (2002) found ungulate herbivory increased N in lichen, but no response in tree leaves in Finland. They concluded that grazing did not affect nutrient acquisition by plants (or the subsequent N content of litter produced). Alternatively, Bolton et al. (1990) documented a clear relationship between vegetation cover and incoming solar radiation and soil moisture, which affected the soil microbial environment and rates of N cycling.

Observed differences in N cycling between vegetated and bare patches of ground suggest effects of microclimate. Ungulates disrupted this relationship by affecting relative amounts and distributions of shrub and herbaceous cover, N distribution, or both, thereby potentially altering ecosystem function by altering soil inputs and environments. Although we did not detect differences in N cycling rates between treatments, the differences in N cycling with respect to vegetation associations and the differences in cover between grazing treatments indicate that the effects of changes in soil microbial activities may be forthcoming. These results contrast significant differences between grazed and ungrazed plots in Yellowstone National Park (Frank and Groffman 1998). However, differences in microbial productivity and N cycling rates in that study were correlated with patterns of soil C and N, and specifically, the labile portion of these elements in the soil profile (Frank and Groffman 1998). The distribution of nutrients and favorable soil microclimates has spatial patterns associated with shrub (Bolton et al. 1990; Bolton et al. 1993; Smith et al. 1994) or grass (Schlesinger et al. 1996; Burke et al. 1998) distributions in these semi-arid systems. Therefore, limiting environmental conditions (climate and soils) and the pre-existing spatial distribution of soil quality may further account for differences between our results and other studies.

Conclusions

We observed that four decades of exclusion of grazing from sagebrush steppe plants changed plant community structure, biological diversity, and ecosystem functions; most notably, a reduction in herbaceous ANPP associated with increased dominance of shrubs. The magnitude of changes in plant community structure appeared to be influenced by the intensity of grazing and the composition of the herbivore community. Alternate states characterized by marked differences in community structure of grazed ecosystems are likely controlled by the combination of differences in abiotic environmental conditions, history of disturbance, and the recent intensity and distribution of herbivores (Laycock 1991; Tausch et al. 1993; Augustine and McNaughton 1998). Our results indicate that changes in structure attributed to differences in ungulate use, especially ratios between shrub and herbaceous cover, are important for predicting ecosystem properties and function.

Acknowledgements The authors are grateful to the Colorado Division of Wildlife, Habitat Division for funding this project, providing logistical support for the research, and preserving the old data and records that enabled re-discovery of these sites. We are also grateful to several diligent crews of seasonal, student employees who helped provide the labor of estimating primary production over two growing seasons, sorting vegetation and soils in the laboratory, assisting in N extractions and running the combustion auto-analyzer. Without their skills, effort, and persistence, this project could not have been completed. We are also grateful to multiple, anonymous reviewers, and the editor, who provided thoughtful comments to improve this manuscript.

References

Aguiar MR, Paruelo JM, Sala OE, Lauenroth WK (1996) Ecosystem responses to changes in plant functional type composition: an example from the Patagonian steppe. J Veg Sci 7:381–390

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62(4):1165–1183

Augustine DJ, McNaughton SJ, Frank DA (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. Ecol Appl 13(5):1325–1337

Bailey RG, Avers PE, King T, McNab WH (eds) (1994) Ecoregions and subregions of the United States (map with supplementary table of map unit descriptions, 1:7,500,000). USDA Forest Service, Washington, D.C.

Beeskow AM, Ellisalde NO, Rostagno CM (1995) Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. J Range Manage 48(6):517–522

Belsky AJ, Blumenthal DM (1997) Effects of livestock grazing on stand dynamics and soils in upland forests of the interior. West Conserv Biol 11(2):315–327

Bolton H, Smith JL, Wildung RE (1990) Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. Soil Sci Soc Am J 54(3):887–891

Burke IC, Lauenroth WK, Vinton MA, Hook PB, Kelly RH (1998) Plant–soil interactions in temperate grasslands. Biogeochemistry 42(1–2):121–143

Burnam KP, Anderson DR (1998) Model selection and inference. A practical information-theoretic approach. Springer, Berlin Heidelberg New York

Chew RM (1982) Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona, 1958–1978. Am Midl Nat 108:159–169

Coughenour MB (1991) Biomass and nitrogen responses to grazing of upland steppe on Yellowstone northern winter range. J Appl Ecol 28(1):71–82

Frank DA (1998) Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. Wildl Soc Bull 26(3):410–418

Frank DA, PM Groffman (1998) Ungulate vs landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79(7):2229–2241

Frank DA, McNaughton SJ (1990) Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. Oikos 57:57–60

Frank DA, McNaughton SJ (1992) The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73(6):2043–2058

Frank D, McNaughton SJ (1993) Evidence for the promotion of above ground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157–161

Frank DA, Inouye RS, Huntly N, Minshall GW, Anderson JE (1994) The biogeochemistry of a north-temperate grassland with native ungulates—nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26(3):163–188

Garcia-Montiel DC, Binkley D (1998) Effect of *Eucalyptus saligna* and *Albizia falcataria* on soil processes and nitrogen supply in Hawaii. Oecologia 113(4):547–556

Gill RB, Beck TDI, Bishop CJ, Freddy DJ, Hobbs NT, Kahn RH, Miller MW, Pojar TM, White GC (1999) Declining mule deer populations in Colorado: reasons and responses: a report to the Colorado Legislature. Unpublished wildlife report. Project number CO W-15. Colorado Division of Wildlife, Colo.

Green RA, Detling JK (2000) Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91(2):280–284

Hillebrand H (2003) Opposing effects of grazing and nutrients on diversity. Oikos 100(3):592–600

Heisler JL, Knapp AK, Briggs JM (2003) Long-term patterns of shrub expansion in a C4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. Am J Bot 90(3):423–428

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60(4):695–713

Hobbs NT (2006) Large herbivores as sources of disturbance in ecosystems. In: Danell K, Pastor J, Bergström R, Duncan P (eds) Large herbivore ecology and ecosystem dynamics. Cambridge University Press, Cambridge, pp 261–288

Hobbs NT, Baker DL, Gill RB (1983) Comparative nutritional ecology of montane ungulates during winter. J Wildl Manage 47:1–16

Hobbs NT, Baker DL, Bear GD, Bowden DC (1996) Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. Ecol Appl 6(1):218–227

Huenneke LF, Anderson JP, Remmenga M, Schlesinger WH (2002) Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. Global Change Biol 8:247–264

Jones A (2000) Effects of cattle grazing on North American arid ecosystems: a quantitative review. West N Am Nat 60(2):155–164

Kufeld RC, Walmo OC, Feddema C (1973) Foods of the Rocky Mountain mule deer. Research paper RM-111. USDA Forest Service

Laycock WA (1991) Stable states and thresholds of range condition on North American Rangelands—a viewpoint. J Range Manage 44(5):427–433

Lecain DR, Morgan JA, Schuman GE, Reeder JD, Hart RH (2000) Carbon exchange rates in grazed and ungrazed pastures of Wyoming. J Range Manage 53(2):199–206

Leriche H, Le Roux X, Desnoyers F, Benest D, Simioni G, Abbadie L (2003) Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. Ecol Appl 13(5):1346–1354

Lett MS, Knapp AK (2006) Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. Am Midl Nat 153:217–231

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23–39

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hoofed mammals. Am Nat 119(6):757–773

Madany MH, West NE (1983) Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64(4):661–667

Manier DJ, Hobbs NT (2006) Large herbivores influence the composition and diversity of shrub steppe communities in the Rocky Mountains, USA. Oecologia 146(4):641–651

McNaughton SJ, Milchunas DG, Frank DA (1996) How can net primary productivity be measured in grazing ecosystems? Ecology 77(3):974–977

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63(4):327–366

Rabe MJ, Rosenstock SS, deVos JC (2002) Review of big-game survey methods used by wildlife agencies of the western United States Source. Wildl Soc Bull 30(1):46–52

Reynolds RT, Trost CH (1980) The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. J Range Manage 33:122–125

Rueth HM, Baron JS (2002) Differences in Englemann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA. Ecosystems 5(1):45–57

Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77(2):364–374

Schultz TT, Leininger WC (1990) Differences in riparian vegetation structure between grazing areas and exclosures. J Range Manage 43:295–299

Singer FJ (1995) Effects of ungulate herbivory and fire on the grasses and shrubs of Yellowstone's Northern Winter Range. Dissertation, Colorado State University, Fort Collins, Colo.

Singer, FJ (1996) Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National Park. In: FJ Singer (ed) Effects of grazing by wild ungulates. Yellowstone National Park technical report. USDI, National Park Service, Natural Resource Information Division

Smith JL, Halvorson JJ, Bolton H (1994) Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. Soil Biol Biochem 26(9):1151–1159

Sommer U (1999) The impact of herbivore type and grazing pressure on benthic microalgal diversity. Ecol Lett 2:65–69

Stark S, Wardle DA, Ohtonen R, Helle T, Yeates GW (2002) The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. Oikos 90(2):301–310

Stohlgren TJ, Falkner MB, Schell LD (1995) A modified-Whittaker nested vegetation sampling method. Vegetation 117:113–121

Stohlgren TJ, Schell LD, Vanden Heuvel B (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecol Appl 9(1):45–64

Tausch RJ, Wigand PE, Burkhardt JW (1993) Viewpoint: plant community thresholds, multiple steady states, vand multiple successional pathways: legacy of the quaternary? J Range Manage 46:439–447

Valentine SC, Bartsch BD (1990) Milk-production by dairy-cows fed legume grains or barley-grain with or without urea as supplements to a cereal hay based diet Australian. J Exp Agric 30(1):7–10

Weber WA, Wittmann RC (2001) Colorado flora, vol. eastern slope and western slope, 3rd edn. University Press of Colorado, Boulder, Colo.

West NE (1988) Intermountain deserts, shrub steppes and woodlands. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, New York, pp 209–230

Willms WD, Dormaar JF, Adams BW, Douwes HE (2002) Response of the mixed prairie to protection from grazing. J Range Manage 55(3):210–216

Zimmerman GT, Neuenschwander LF (1984) Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir Ninebark habitat type. J Range Manage 37(2):104–110



The Food Habits and Summer Distribution of Juvenile Sage Grouse in Central Montana

J. G. Peterson

The Journal of Wildlife Management, Vol. 34, No. 1. (Jan., 1970), pp. 147-155.

Stable URL:
http://links.jstor.org/sici?sici=0022-541X%28197001%2934%3A1%3C147%3ATFHASD%3E2.0.CO%3B2-2

The Journal of Wildlife Management is currently published by Alliance Communications Group.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/acg.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Tue May 15 11:47:51 2007

THE FOOD HABITS AND SUMMER DISTRIBUTION OF JUVENILE SAGE GROUSE IN CENTRAL MONTANA[1]

J. G. PETERSON, Montana Fish and Game Department, White Sulphur Springs

Abstract: The food habits of juvenile sage grouse (*Centrocercus urophasianus*) were studied in central Montana during the summers of 1966 and 1968. Forbs averaged 75 percent of the diet of 127 juveniles through 12 weeks of age. The flower buds and leaves of common dandelion (*Taraxacum officinale*) and common salsify (*Tragopogon dubius*) were the most highly preferred and utilized forbs, comprising 25 and 15 percent of the diets, respectively. Other forbs commonly utilized were prairie pepperweed (*Lepidium densiflorum*), prickly lettuce (*Lactuca serriola*), alfalfa (*Medicago sativa*), curlcup gumweed (*Grindelia squarrosa*), and fringed sagewort (*Artemisia frigida*). Big sagebrush (*A. tridentata*) received little use until the birds were 11 weeks old. Insect use declined steadily from a high of 60 percent of the diet in 1-week chicks to 5 percent in 12-week-old juveniles. Observed brood locations, after chicks were 2–3 weeks old, were less frequent on the sagebrush-grassland benches and more frequent on lower areas until, by September, the majority of broods were located on bottomlands. Sagebrush, 6–18 inches high, was most prevalent at brood sites used during morning and evening activity periods. Important components of juvenile sage grouse habitat in this area appear to be an abundance and diversity of forbs and densities of sagebrush ranging from 1–20 percent.

Range management practices in many areas of the West have shown an increasing trend toward removal or manipulation of stands of sagebrush. The Montana Fish and Game Department and the United States Bureau of Land Management initiated a study in 1965 to determine the ecological effect of sagebrush manipulation.

As part of this project, my study was conducted during the summers of 1966 and 1968 to determine the food habits of juvenile sage grouse.

Past studies of food habits have indicated a high use of forbs and varying amounts of animal matter by adult sage grouse during the summer months, as opposed to almost total dependence upon sagebrush during the rest of the year (Rasmussen and Griner 1938:855–858; Patterson 1952:203). It has also been shown that juvenile sage grouse rely heavily upon forbs and animal matter during the first few months of their lives (Rasmussen and Griner 1938:855–858; Patterson 1952:201, 203; Klebenow and Gray 1967:80–83). My study placed emphasis on the availability of the plant food items.

I wish to extend sincere appreciation to R. L. Eng, Montana State University, for technical supervision and guidance in preparation of the manuscript. Also, I appreciate the technical assistance and advice provided by: R. J. Mackie, formerly with the Montana Department of Fish and Game; D. Pyrah, T. Mussehl, K. Greer, all with the Montana Department of Fish and Game, and W. E. Booth, Montana State University.

THE STUDY AREA

The study area is located in central Montana near the town of Winnett. This region was described by Gieseker (1938) as having a semiarid climate, great temperature extremes, and a large number of sunny days. The average precipitation for the study area from June to September each year is 6.74 inches. During the first summer of the study, precipitation was 4.3

[1] A joint contribution from Montana State University, Agricultural Experiment Station, Project No. MS400, Paper No. 108 Journal Series and the Game Management Division, Federal Aid Projects W-105-R-1 through 4, Montana Fish and Game Department.

inches below normal, while during the second summer it was 3.2 inches above. Average summer temperature for the area is 65.4 F (U. S. Department of Commerce, 1966 and 1968).

Plants dominating the higher prairie elevations included the shrubs big sagebrush and broom snakeweed (*Gutierrezia sarothrae*). The predominant forbs were fringed sagewort, plains pricklypear (*Opuntia polycantha*), plantain (*Plantago* spp.), American vetch (*Vicia americana*), and Hood's phlox (*Phlox hoodii*). Several species of wheatgrass (*Agropyron* spp.) were the most predominant grasses. Other common grass species included blue grama (*Bouteloua gracilis*), Junegrass (*Koeleria cristata*), bluegrass (*Poa* spp.), needle and thread (*Stipa comata*), and green needlegrass (*S. viridula*).

The lower elevations, especially those adjacent to creek bottomlands, were often dominated by shrubs such as big sage, silver sage (*Artemisia cana*), greasewood (*Sarcobatus vermiculatus*), and rubber rabbitbrush (*Chrysothamnus nauseosus*). Common dandelion, yarrow (*Achillea millefolium*), and curlcup gumweed were common forbs. Wheatgrasses were the major grasses found at the lower elevations. Others commonly found were foxtain barley (*Hordeum jubatum*), brome (*Bromus* spp.) and desert saltgrass (*Distichlis stricta*).

Many of the stream bottomlands have been planted to alfalfa, whereas the adjoining sagebrush-grasslands are used almost exclusively for livestock grazing.

METHODS

Initially, all portions of the study area were searched by vehicle for sage grouse broods during the morning and afternoon activity periods. Morning searches were later abandoned after it was discovered that crop contents were minimal from birds collected at this time.

Most chicks were shot, but those less than 2 weeks old were easily caught by hand.

Each collection was made in essentially the same manner. After a brood was discovered, the birds' feeding activities were carefully observed with a 15–60× variable spotting scope and/or a 7 × 35 binocular. Observations were made for approximately 30 minutes at a sufficient distance to prevent disturbance. At the end of this period, I collected one of the chicks, marked the feeding area with stakes for later vegetational analysis, and briefly described the vegetational and physical characteristics of the site.

The age of each bird collected was determined by measurements of certain external features: tail length, foot length, leg length, and the stage of molt found on the primary wing feathers (Eng 1955, Pyrah 1963). Sex was determined by internal examination. The crop and gizzard were marked and preserved in 10 percent formalin.

Crop and gizzard analyses were conducted after the field season. Normally only the crop was considered since the items found in it should have been most representative of items being fed upon immediately prior to collection. Measurements of food items were made volumetrically by the displacement of water. Measurements within each age-class were grouped by use of the aggregate volume method, while those between age-classes were grouped by the aggregate percentage method (Martin et al. 1946). Supplemental crops were obtained during both years from predator and road kills throughout the summer, and hunter-killed birds on the opening day of grouse season.

Vegetation in each feeding area was analyzed within several days after each chick collection. A method similar to that

used by Daubenmire (1959) was utilized to determine canopy coverage. Twenty 2- × 5-dm plots were placed at 5-ft intervals along a 100-ft tape. This tape was placed along the observed path the brood used while feeding. Within these plots, the coverage of each plant species was visually determined. Shrub characteristics such as crown coverage and average heights, were recorded by the use of the line intercept (Canfield 1941) along the 100-ft tape. Plant nomenclature is that of Booth (1950) and Booth and Wright (1959).

In a food habits study, the availability of an item and its observed use by the animal are two of the more important factors to be considered. Therefore the percent volume of each plant food item and the percent canopy coverage of the same species in the feeding area were used in calculating a preference index. The percent volume of the food item found in the crop was divided by the percent canopy coverage of that same plant and the quotient was used as the preference index. The larger the index number, the greater is the preference.

To supplement the food habits study, data on the spring and summer distribution of sage grouse broods with respect to vegetative types along two observation routes were gathered. These routes followed roads and trails through sagebrush-grasslands, benchlands, and stream bottoms, and were traversed once a week throughout the summer. The War Horse route, 45.1 miles long, was north of Winnett, and the Yellow Water Triangle route, 50.4 miles, was south of Winnett. These routes, used only in the mornings, were completed before the broods ceased their morning activities.

When a brood was observed, the birds were flushed, counted, and the spot where the hen was first seen was marked. Notation was then made of the characteristic features of the surrounding area in the same manner as described for chick-collection sites.

After a route was finished, vegetation analysis was conducted at each brood site. The methods employed were basically similar to those used at the collection sites with the sample plots placed on lines radiating out from the location of the hen rather than along an observed area of feeding.

RESULTS

During the 2 summers of the study, I analyzed the crop contents from 151 juvenile and 32 adult sage grouse. The juveniles were separated into weekly age-classes. The frequency and volume of food items found in 127 of these birds are presented by 4-week age divisions in Table 1.

Although grouse older than 12 weeks were collected, the primary interest of this study centered around the food habits of juveniles and this age was decided upon as a suitable breaking point. Rasmussen and Griner (1938:855) found the food habits of juveniles to parallel those of adults after 3 months of age. The results of the food analysis of adults and juveniles 13 weeks and older are presented in Table 2.

Considering all birds through 12 weeks of age, the average diet during the two summers consisted of 76 percent vegetable and 24 percent animal matter (Table 1).

The two most important plant items in the diet throughout the two summers were common dandelion and common salsify. Dandelion was found in 55 percent of the grouse analyzed, and salsify was found in 63 percent, while both averaged the two largest individual crop volumes of all juveniles both years.

Five other commonly utilized plants occurred more periodically in the chicks' diets. Prairie pepperweed was very important in the younger age-classes. During the first 5 weeks, this item was utilized by 44 per-

Table 1. Percent frequency and volume of food items commonly utilized by 1–12-week-old sage grouse collected during 1966 and 1968.

Food Item	Age (Weeks) 1–4 (26)[a] Percent Freq./Vol.	5–8 (47) Percent Freq./Vol.	9–12 (54) Percent Freq./Vol.	Total[b] Freq./Vol.
FORBS				
Taraxacum officinale	63/33	59/23	43/19	55/25
Tragopogon dubius	46/9	83/30	60/5	63/15
Lactuca serriola	–	27/9	60/26	29/12
Lepidium densiflorum	48/22	2/1	2/tr	17/8
Artemisia frigida	6/tr	35/3	50/19	30/7
Grindelia squarrosa	9/tr	28/3	39/4	25/2
Medicago sativa	–	21/2	22/2	14/1
Unidentified forbs	37/3	28/1	30/tr	32/1
Camelina microcarpa	9/1	2/tr	–	4/tr
Achillea millefolium	–	2/tr	8/1	3/tr
SHRUBS				
Artemisia tridentata	6/tr	2/tr	41/3	16/1
Rhus trilobata	–	3/3	–	1/1
GRASSES				
Triticum aestivum	–	–	9/3	3/1
TOTAL VOLUMES OF TRACE MATERIAL	2	1	1	1
TOTAL PERCENT PLANT VOLUME	70	76	83	76
ANIMAL MATTER				
Orthoptera	29/1	40/21	37/17	35/13
Coleoptera	78/8	44/1	18/tr	47/3
Hymenoptera	76/7	50/1	45/tr	53/3
Immature insects	54/5	23/1	–	26/2
Unidentified insects	34/1	21/tr	9/tr	21/tr
TOTAL VOLUMES OF TRACE MATERIAL	8	–	–	3
TOTAL PERCENT ANIMAL VOLUME	30	24	17	24

[a] Number of birds.
[b] Totals are derived by aggregating the percentages from every week-class, thereby eliminating any bias introduced by the individual sample size and crop holding capacity of each age-class.

cent of the grouse and averaged 15 percent of the total volume, while occurring in only trace amounts in older birds. Prickly lettuce, fringed sagewort, curlcup gumweed, and alfalfa were not utilized to any extent until the fifth or sixth week.

Big sagebrush never became an important constituent of the chicks' diet, occurring in only 16 percent of the birds and averaging 1 percent of the total volume for both summers. Traces of this shrub (the leaves) were found in younger birds, but it only occurred in quantity in juveniles over 10 weeks of age.

Animal matter (primarily insects) was the most important constituent of the diet during the first week of age, totaling 60 percent of the crop volume. However, this sample consisted of only two chicks. This high animal use dropped to 33 percent of

Table 2. Percent volume and frequency of common plant and animal food items found in sage grouse juveniles 13 weeks and older and adults in 1966 and 1968.

FOOD ITEM	JUVENILES (13–16+ Weeks)[a] (24)[b] Freq./Vol.	ADULTS August (18) Freq./Vol.	ADULTS September (14) Freq./Vol.
PLANT			
Lactuca serriola	51/38	37/11	29/35
Taraxacum officinale	67/30	70/33	59/4
Artemisia frigida	26/13	63/11	37/2
Medicago sativa	43/6	40/8	4/tr
Tragopogon dubius	41/6	60/10	59/1
Artemisia tridentata	27/2	37/5	59/3
Achillea millefolium	3/tr	17/tr	54/38
Other Plant Volume	2	13	17
Total Plant Volume	97	81	100
ANIMAL			
Orthoptera	14/3	30/17	–
Other Animal Volume	–	2	–
Total Animal Volume	3	19	0

[a] It is difficult to place old juveniles into exact week-classes. However, there were few birds past 16 weeks of age.
[b] Number of birds.

the volume in the 2-week-old birds. The percentage of animal matter in the diet for the 3–11-week-old birds remained quite constant but at a lower level. In birds 12 weeks old, animal matter totaled 5 percent of the crop volume.

Orthoptera (primarily grasshoppers), Coleoptera (beetles), and Hymenoptera (primarily ants), were the most important insects in the diet. Grasshoppers constituted the largest animal portion of the diet, heavy utilization beginning primarily in the 5-week chicks. From that age through 12 weeks, they occurred in 38 percent of the crops and averaged 19 percent of the volume.

Beetles were utilized during the entire summer. However, only 19 percent of the juveniles from 7–12 weeks of age ate beetles, while 73 percent utilized this group of insects during the first 6 weeks, when they averaged 5 percent of the crop volume.

Ants were utilized heavily by the young chicks, but added little to the volume. While ants were found in 76 percent of the crops and averaged 7 percent of the volume in birds 1–4 weeks old, they rarely occurred in more than trace amounts in older juveniles.

A marked contrast in the use of dandelion and grasshoppers was observed between the 2 years. The amount of dandelion found in the crops in 1968 was over twice that found in 1966. Grasshoppers were very prominent in the crops of birds collected in 1966, but only occurred in trace amounts in 1968.

Food Item Preference

According to the calculated preference indices obtained from 81 sage grouse juveniles and their corresponding collection sites, the five most preferred plants utilized by each 2-week-age grouping of chicks were determined (Table 3).

Differences in physical structure between plant species introduces some error to these data. For example, leaves were the most common part of dandelion found in the

Table 3. The five most preferred plant species in each 2-week age division of juvenile sage grouse, 1966 and 1968 (rated by preference indices).[a]

Food Item	Age (Weeks) 1–2 (8)[b]	3–4 (14)	5–6 (17)	7–8 (16)	9–10 (11)	11–12 (9)	13–14 (6)	Total
Tragopogon dubius	3	5	4	4[c]	4	1	5	26
Taraxacum officinale	5	3	3	3	2	5	3	24
Artemisia frigida	–	–	–	2	5	4	4	15
Lactuca serriola	–	–	5	5	3	–	–	13
Medicago sativa	–	–	2	–	–	3	2	7
Lepidium densiflorum	4	2	–	–	–	–	–	6
Grindelia squarrosa	2	1	–	1	1	–	–	5
Camelina microcarpa	–	4	–	–	–	–	–	4
Achillea millefolium	–	–	–	–	–	2	–	2
Vicia americana	1	–	–	–	–	–	–	1
Lactuca pulchella	–	–	1	–	–	–	–	1
Carex spp.	–	–	–	–	–	–	1	1

[a] The number assigned to each species, in descending order of importance, indicates its status as a preferred plant food item.
[b] Sample size.
[c] *Rhus trilobata* has the second highest index number in the 7–8-week division, but was not considered as it only occurred in the crop of one bird.

crops although flower buds were the main parts taken from salsify. It would take many dandelion leaves from several plants to equal the volume displaced by one or two salsify flower buds from one plant. This could tend to give salsify a higher preference rating than dandelion at certain sites, even if a chick spent equal or more time eating dandelion leaves. Since this study gave the availability and abundance factor of each plant species as much consideration as possible in the selection of food items by juvenile sage grouse, the method used was considered applicable.

Brood Distribution

The general vegetative types in which broods were located, obtained only in 1968, are presented for each month (June through September) in Table 4. The average percent of each type found along both observation routes is also presented. The sagebrush-grassland type received the highest average use for the entire summer. Use of this type decreased from 100 percent in June to 50 percent in September. Corresponding with this decrease was an increased use of greasewood and grassland types. This increase, particularly in the case of greasewood, was correlated with brood movements from higher benchland types, to more mesic bottomland sites as the summer progressed.

Ninety-one canopy coverage transects were run at brood locations along the observation routes during both summers. The vegetative measurements gathered at each of these sites were combined for each month and compared between years.

The combined canopy coverage of forbs for both summers averaged 33 percent. The coverage during the wet summer of 1968 was considerably higher than in the previous year when precipitation was low. Vegetation in general remained greener later into the summer of 1968 than in 1966. This difference was particularly prominent during July when over twice as much forb cover was present at brood sites in 1968 (53 percent) than was present in 1966, and again in August, when forb cover was three times greater in 1968 (48 percent) than in 1966. This trend appeared reversed in September, but only small samples were

Table 4. Vegetative types at brood locations along observation routes in 1968.

	NUMBER OF SITES	VEGETATIVE TYPE			
		Percent Sagebrush-Grassland (69)[a]	Percent Grassland (10)	Percent Greasewood (14)	Percent Miscellaneous (8)
MONTH					
June	(11)	100	–	–	–
July	(19)	74	5	11	11
August	(16)	63	18	18	–
September	(4)	50	25	25	–

[a] The average percent of each vegetative type found along both routes.

obtained. The abundance of sweet clover (*Melilotus officinalis*) was the single biggest reason for greater forb cover in 1968 than in 1966.

The crown coverage of sagebrush found on brood sites for the 2 years shows an average cover of 6 percent from June through August, increasing to an average of 12 percent during September.

The average heights of the sagebrush stands found at brood sites in 1966 increased from an average of 16 inches in June to 20 inches in September. In 1968, sagebrush heights of 6–12 and 12–18 inches were the dominant height classes at brood sites each month. In Montana, Martin (1965:20) found big sagebrush plant heights ranging from 9–15 inches at locations of young broods.

DISCUSSION

Forbs are important in the summer diets of juvenile sage grouse. The availability of, and seeming preference for, parts of certain forbs played an important role in the seasonal use of these plants as well as in the distribution of the birds.

The higher utilization of dandelion in 1968, as compared to 1966, was apparently due to above normal precipitation, which caused this forb to be particularly prevalent at most brood locations. This may have been an important factor in the wide brood distribution throughout the sagebrush-grassland areas during the summer months of 1968. The seed pods of prairie pepperweed were a very important constituent of the diet of the youngest grouse. The small size of this plant placed these pods within easy reach. In most instances, this plant became desiccated and unavailable as a food source by the time the chicks were 5 or 6 weeks old. Availability also appeared to be the main factor governing the use of prickly lettuce. Although a few leaves of this plant were taken earlier, the flower buds became available near the end of July and were heavily utilized by August. Although this plant began to desiccate in certain areas and become less available by the first of September, it still constituted an important item in the diet of birds 11 through 12 weeks of age.

Availability did not appear to be the most important factor governing the utilization of fringed sagewort. Although this species was commonly found at nearly every feeding site and/or brood location during each month of the study, it did not appear in the crops until chicks were 4 weeks old, and then only as a trace. Thereafter each successive week-class of juveniles utilized increasingly larger amounts of fringed sagewort leaves through the 11–12-week group. The juveniles increased use and apparent preference for fringed sagewort with the advance of summer may be

related to their future diet. Since fringed sagewort is a relative of big sagebrush and is normally present as a perennial, it conceivably might be used as a transitional food item between the summer diet consisting of forbs and the winter diet of big sagebrush.

Big sagebrush received little use by juvenile sage grouse during the summer. Increased use of this plant was noted in older birds, composing as much as 11 percent of the diet in the 11-week-old juveniles. However, it comprised only 1 percent of the crop volume in 12-week-old birds.

Alfalfa was not utilized to any extent until later in the summer when many of the birds began feeding in hay meadows. Even then, alfalfa never became more than the third most preferred plant food item or comprised more than 7 percent of the volume in any single week-age class. When I observed and collected juveniles feeding in alfalfa fields, dandelion and salsify were quite frequently the major items in the crops. Thus it would appear that in most instances, sage grouse are attracted to hay meadows by the lush vegetational aspect, and not specifically to alfalfa as a food item.

Grass leaves occurred in the crops of nearly every age-class, but never constituted more than a trace of the volume in any bird. It is believed that most of this use occurred incidentally while feeding on other species.

Considerable difference was observed in the percentage of animal matter in the diet between 1966 and 1968. This difference was attributed to heavy utilization of grasshoppers in 1966, which in 1968 constituted only a trace. There appeared to be an abundance of grasshoppers during most of the 1966 summer season. Most of the plants on the study area became desiccated early that year. This condition tended to concentrate both grouse and grasshoppers into common areas of succulent vegetation, and therefore made these insects readily available to the birds. By contrast, in 1968, the grouse were still distributed throughout the study area during mid- and late summer, presumably due to the above normal precipitation and resulting forb cover. If the grasshopper population was equally distributed, there would be less chance of high numbers of grasshoppers being available to individual birds, even if the insect population was the same for both years.

During the summer, juvenile grouse on the study area preferred forbs for food and utilized sagebrush for cover. A desirable forb composition in brood habitat should be sufficiently diverse to provide a variety of succulent plants throughout the season. Range manipulation which would eliminate sagebrush and reduce the abundance and variety of forbs, would lower the ability of this range to support juvenile sage grouse.

LITERATURE CITED

BOOTH, W. E. 1950. Flora of Montana. Part I, Conifers and Monocots. Research Foundation, Montana State College, Bozeman. 232pp.

———, AND J. C. WRIGHT. 1959. Flora of Montana. Part II, Dicotyledons. Research Foundation, Montana State Coll., Bozeman. 250pp.

CANFIELD, R. H. 1941. Application of the line interception method in sampling range vegetation. J. Forestry 39(4):388–394.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33 (1):43–64.

ENG, R. L. 1955. Wildlife Investigation. Montana Fish and Game Dept. Job Completion Rept., Proj. W-74-R-1, Job 3.1. 6pp.

GIESEKER, L. F. 1938. Soils of Petroleum County. Montana Agr. Expt. Sta. Bull. 363. 46pp.

KLEBENOW, D. A., AND G. M. GRAY. 1967. Food habits of juvenile sage grouse. J. Range Mgmt. 21(2):80–83.

MARTIN, A. C., R. H. GENSCH, AND C. P. BROWN. 1946. Alternative methods in upland gamebird food analysis. J. Wildl. Mgmt. 10(1): 8–12.

MARTIN, N. S. 1965. Effects of sagebrush manipulation on sage grouse. M. S. Thesis. Montana State Coll., Bozeman. 38pp.

PATTERSON, R. L. 1952. The sage grouse in Wyoming. Sage Books, Inc., Denver. 341pp.
PYRAH, D. B. 1963. Sage grouse investigations. Idaho Fish and Game Dept., Job Completion Rept., Proj. W-125-R-2. 71pp.
RASMUSSEN, D. I., AND L. A. GRINER. 1938. Life history and management studies of the sage grouse in Utah, with special reference to nesting and feeding habits. Trans. N. Am. Wildl. Conf. 3:852–864.
U. S. DEPARTMENT OF COMMERCE. 1966. Climatological data Montana 69(6–9):109–203.
———. 1968. Climatological data Montana 71 (6–9):109–209.

Received for publication June 25, 1969.

BOBWHITES AS POSSIBLE RESERVOIR HOSTS FOR BLACKHEAD IN WILD TURKEYS[1]

FOREST E. KELLOGG, Southeastern Cooperative Wildlife Disease Study, School of Veterinary Medicine, University of Georgia, Athens
W. MALCOLM REID, Department of Poultry Science, University of Georgia, Athens

Abstract: Blackhead disease, caused by *Histomonas meleagridis*, occurs regularly in wild turkey (*Meleagris gallopavo*) populations in the southeastern United States. Experimental studies proved that an isolate of *H. meleagridis* originating from chicken cecal worm (*Heterakis gallinarum*) eggs caused blackhead in bobwhites (*Colinus virginianus*) and domestic turkeys. Bobwhites were less susceptible than turkeys to death from blackhead and were better carriers of the disease. Turkeys placed in a pen containing infected quail died from blackhead within 70 days. The incidence of blackhead in wild turkey populations is probably related to the number and species of other wild bird hosts in the area as well as to wild turkey density and proximity of domestic poultry.

This paper is a report on experimental studies concerning possible blackhead interrelationships between wild turkeys and bobwhites.

There has been much concern about the factors which limit or decimate wild turkey populations. Disease has often been cited as such a factor. Kozicky (1948:116) felt that disease played an important role in limiting fall turkey populations in Pennsylvania and that if hunting pressure were withdrawn, the turkey population still would be limited by disease. He cited areas in Pennsylvania where the population level had decreased after being closed to hunting for 2 years. Bailey and Rinell (1968:34) cited instances of problems with blackhead, also known as histomoniasis or infectious enterohepatitis, in Michigan, Virginia, West Virginia, and Wisconsin. Craig and Barkalow (1950) reported blackhead in North Carolina wild turkeys. Stoddard (1935) noted that blackhead was the only disease that he had seen in wild turkeys in southwest Georgia. In the past 15 years, the wild turkey population in southwest Georgia has declined severely and blackhead has been the usual diagnosis when sick birds were found. During this 15-year period, habitat conditions have remained grossly similar but bobwhites have become more abundant.

Recent knowledge concerning the etiology and dissemination of blackhead was reviewed by Reid (1967). *H. meleagridis*, the protozan etiologic agent of blackhead,

[1] This study was supported by an appropriation from the Congress of the United States to the Southeastern Cooperative Wildlife Disease Study, University of Georgia. Funds administered and research coordinated under Federal Aid in Wildlife Restoration Act (50 Stat. 917), through Contract No. 14-16-0008-676, U. S. Department of the Interior, and Tall Timbers Research Station, Tallahassee, Florida.

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations | Graduate Studies

12-2010

Factors Affecting Gunnison Sage-Grouse (*Centrocercus minimus*) Conservation in San Juan County, Utah

Phoebe R. Prather
Utah State University

Follow this and additional works at: https://digitalcommons.usu.edu/etd

 Part of the Natural Resources and Conservation Commons

Recommended Citation

Prather, Phoebe R., "Factors Affecting Gunnison Sage-Grouse (*Centrocercus minimus*) Conservation in San Juan County, Utah" (2010). *All Graduate Theses and Dissertations*. 827.
https://digitalcommons.usu.edu/etd/827

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



FACTORS AFFECTING GUNNISON SAGE-GROUSE (*CENTROCERCUS MINIMUS*) CONSERVATION IN SAN JUAN COUNTY, UTAH

by

Phoebe R. Prather

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

_____	_____
Dr. Terry A. Messmer Major Professor	Dr. Christopher A. Call Committee Member
_____	_____
Dr. Frederick D. Provenza Committee Member	Dr. Eugene W. Schupp Committee Member
_____	_____
Dr. Tim B. Graham Committee Member	Dr. Byron Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2010

Copyright © Phoebe Prather 2010

All Rights Reserved

ABSTRACT

Factors Affecting Gunnison Sage-Grouse (*Centrocercus minimus*)

Conservation in San Juan County, Utah

by

Phoebe R. Prather, Doctor of Philosophy

Utah State University, 2010

Major Professor: Terry A. Messmer
Department: Wildland Resources

Due to loss of habitat, Gunnison sage-grouse (*Centrocercus minimus*) currently occupy 8.5% of their presumed historical range. One population survives in Utah, occurring in San Juan County. The Gunnison Sage-grouse Rangewide Conservation Plan and the San Juan County Gunnison Sage-grouse Conservation Plan recommended management strategies to address identified conservation threats to the Utah population. I addressed three conservation strategies identified in the plans: 1) creation and enhancement of brood-rearing areas; 2) assessment of habitat conditions within the Gunnison Sage-grouse Conservation Area; and 3) prevention or reduction of perching events by avian predators on distribution line power poles.

From 2007-2009, I addressed the conservation strategy of creating mesic brood-rearing areas in Conservation Reserve Program fields and native sagebrush areas by evaluating the role of irrigation and dormant season cattle grazing on habitat. Vegetation and arthropod diversity in irrigated versus non-irrigated plots did not differ ($p>0.01$).

Conservation Reserve Program plots exhibited greater arthropod abundance and cover of perennial grass than the native sagebrush plots, but lower diversity of perennial grasses and abundance and diversity of forbs ($p<0.01$).

The second conservation strategy I addressed was the completion of an assessment of habitat conditions within the Gunnison Sage-grouse Conservation Area. I measured vegetation conditions within habitat occupied and unoccupied by Gunnison sage-grouse. Cover and height of grasses exceeded guidelines for occupied and unoccupied habitats. Forb cover was below recommended guidelines in occupied habitat. Sagebrush cover was below guidelines for winter habitat. Habitat restoration efforts should focus on retaining existing sagebrush cover and establishment of sagebrush, forb, and grass cover within Conservation Reserve Program fields.

The third conservation strategy I evaluated was the retrofitting of distribution line power poles with perch deterrents to discourage avian predators from perching. I evaluated the efficacy of five perch deterrents. The perch deterrents did not mitigate potential avian predators from perching. A deterrent designed for insulators, in combination with physical deterrents we tested, has potential to prevent perching.

These studies provided a sound first step that can be built upon by the Monticello/Dove Creek Local Working Group to improve habitat conditions, reduce the threat of avian predation, and plan future conservation activities within the Conservation Area.

(138 pages)

ACKNOWLEDGMENTS

I would like to thank the Bureau of Land Management, the Natural Resources Conservation Service, the Endangered Species Mitigation Fund, and the Jack H. Berryman Institute for providing funding. I would like to give special thanks to my advisor, Dr. Terry Messmer, for his support and guidance throughout this process. This project also benefited from the direction of my committee members Dr. Tim Graham, Dr. Christopher Call, Dr. Fredrick Provenza, and Dr. Eugene Schupp.

Cooperation from the members of the Monticello/Dove Creek Gunnison Sage-Grouse Working Group has been greatly appreciated. Specifically, I would like to recognize Tammy Wallace, Guy Wallace, Doug Christensen, and Don Andrews for their support and assistance.

I would like to give special thanks to Tammy Wallace, Guy Wallace, Todd Black, Erin Colin, Steve Duke, and the Canyon Country Youth Corp for their help at odd hours and in unpleasant conditions.

Special thanks to my family and friends for their support and encouragement throughout my time at Utah State University

Phoebe R. Prather

CONTENTS

Page

ABSTRACT iii

ACKNOWLEDGMENTS v

LIST OF TABLES ix

LIST OF FIGURES xi

CHAPTER

1. INTRODUCTION 1

BACKGROUND 1

Species Description 1
Species Distribution 2
Species Status and Conservation 3
Gunnison Sage-grouse Rangewide Conservation Plan 6
San Juan County Gunnison Sage-grouse Conservation Plan 7
Utah Population Status 8
Ecology of the Utah Population 10

STUDY PURPOSE 16
LITERATURE CITED 17

2. EFFECT OF IRRIGATION AND DORMANT SEASON CATTLE GRAZING ON VEGETATION DIVERSITY AND ARTHROPOD ABUNDANCE IN CONSERVATION RESERVE PROGRAM AND NATIVE SAGEBRUSH IN SAN JUAN COUNTY, UTAH 20

ABSTRACT 20
INTRODUCTION 21

Sage-grouse Brood-rearing Habitats 22
Gunnison Sage-grouse Brood-rearing Habitat in Utah 24
The Farm Program and Sage-grouse Conservation 25
Land Use Changes in San Juan County and Gunnison Sage-grouse 26
CRP and Sage-grouse 27

STUDY PURPOSE....29
STUDY AREA....29
METHODS....32

Experimental Design....32
Irrigation....33
Vegetation Monitoring....35
Arthropod Surveys....36
Sage-grouse Pellet Counts....38
Dormant Season Cattle Grazing....39

DATA ANALYSIS....39
RESULTS....40

Vegetation Response....40
Arthropod Response....44
Sage-grouse Use....45

DISCUSSION....46
MANAGEMENT IMPLICATIONS....52
LITERATURE CITED....53

3. ASSESSMENT OF VEGETATION CONDITIONS OF SAGEBRUSH HABITATS WITHIN THE GUNNISON SAGE-GROUSE (*CENTROCERCUS MINIMUS*) CONSERVATION AREA IN SAN JUAN COUNTY, UTAH....58

ABSTRACT....58
INTRODUCTION....59
STUDY AREA....61
METHODS....62
DATA ANALYSIS....66
RESULTS....66

Occupied Habitat....67
Unoccupied Habitat....67

DISCUSSION....68
MANAGEMENT IMPLICATIONS....74
LITERATURE CITED....74

4. RAPTOR AND CORVID RESPONSE TO POWER DISTRIBUTION LINE PERCH DETERRENTS IN UTAH....77

ABSTRACT....77
INTRODUCTION....78
STUDY AREA....79
METHODS....80
RESULTS....84
DISCUSSION....86
MANAGEMENT IMPLICATIONS....89
LITERATURE CITED....90

5. CONCLUSIONS....93

LITERATURE CITED....98

APPENDICES....101

CURRICULUM VITAE....119

LIST OF TABLES

Table Page

3.1. Average percent cover and height of vegetation in occupied and unoccupied habitat in the Gunnison Sage-grouse (*Centrocercus minimus*) Conservation Area in San Juan County, Utah, 2009, reported with 95% confidence intervals. Occupied habitat was defined as land within the Gunnison Sage-grouse Conservation Study Area. Unoccupied habitat was defined as areas that once supported sage-grouse or were in close proximity to areas that support or once-supported sage-grouse. Unoccupied habitat fell within the Conservation Area and Core Conservation Area. Current habitat conditions were compared to habitat guidelines stated in the Gunnison Sage-grouse Rangewide Conservation Plan (GSRSC 2005) 70

4.1. Number of perching events (n) and percentage of perching events (%) by golden eagles, common ravens, and rough-legged hawks recorded documented on each perch deterrent tested and control power poles, and the estimated treatment mean ($\bar{x}$) with standard error (SE). San Juan County, Utah 2007 and 2008. The perch deterrents tested included: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL) and c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT)..... 86

4.2. Number of perching events (n) documented for golden eagles, common ravens, and rough-legged hawks by perch deterrent type and control, and *F*-statistics (*F*) and *P*-values (*P*), San Juan County, Utah 2007 and 2008. The perch deterrents tested included: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL), and c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT)..... 87

A.1. Vegetation mixture seeded on Conservation Reserve Program (CRP) lands within the Gunnison Sage-grouse Conservation Area in San Juan County, Utah (SWOG 2000) 102

A.2. Shrubs, perennial grasses, annual grasses, and forbs measured in Conservation Reserve Program (CRP) and native sagebrush within the Gunnison Sage-grouse Conservation Study Area during the summers of 2007, 2008, and 2009. San Juan County, Utah 103

A.3. Tables reporting Type 3 tests of fixed effects and covariance parameter estimates of percent cover, height, and forage production of sagebrush, perennial grass, annual grass and forbs, and arthropod abundance in Conservation Reserve Program and native sagebrush plots for each water treatment (once a week, every 2 weeks, every 3 weeks) and grazing treatment (grazed, not grazed) in 2007, 2008, and 2009, San Juan County, Utah (p<0.001).....104

A.4. Copyright release letters of the *Journal of Wildlife Management* and Allen Press allowing the republication of: Prather, P.R. and T.A. Messmer. 2010. Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah. *Journal of Wildlife Management* 74(4): 796-800.....117

LIST OF FIGURES

Figure Page

1.1. Current and historical Gunnison sage-grouse (*Centrocercus minimus*) range (Gunnison Sage-grouse Rangewide Steering Committee 2005) 3

1.2. Locations of current Gunnison sage-grouse (*Centrocercus minimus*) populations. (Gunnison Sage-grouse Rangewide Steering Committee 2005) 4

1.3. Historic (left) and current (right) distribution of Greater sage-grouse (*Centrocercus urophasianus*) and Gunnison sage-grouse (*C. minimus*) in Utah (Beck et al. 2003). Gunnison sage-grouse distributions in San Juan County, Utah are circled.....9

1.4. Gunnison Sage-grouse (*Centrocercus minimus*) lek counts from San Juan County, Utah. Maximum number of males observed is recorded. Data from Hickman and BLM leks have been combined because of daily movements of males between these two leks (SWOG 2008)…….…….....10

1.5. Gunnison sage-grouse (*Centrocercus minimus*) Conservation Area, San Juan County, Utah (Lupis 2005) 11

2.1. Agricultural lands enrolled in the Conservation Reserve Program under the conservation priority initiative in the Conservation Study Area, San Juan County, Utah (Lupis 2005).....28

2.2. Gunnison Sage-grouse Conservation Area, San Juan County, Utah (Lupis 2005) 31

2.3. Experimental design schematic showing the layout of 4 blocks each containing 3 randomly assigned watering treatments (once a week, every 2 weeks, every 3 weeks) and control (no water), ungrazed and grazed treatments, and location of arthropod trapping grid, vegetation transects, and rain-bird sprinkler. Each layout occurs in the Conservation Reserve Program and native sagebrush habitats. San Juan County, Utah, 2007-2009 34

2.4. Arrangement of pitfall traps at each terrestrial arthropod sampling plot of the study, San Juan County, UT 2007-2009 (Graham et al. 2008).....38

3.1. Gunnison Sage-grouse Conservation Area, San Juan County, Utah (Lupis 2005) 63

3.2. Buffer distances from active and historic leks to show seasonal movements of Gunnison sage-grouse (*Centrocercus minimus*) in and around the Conservation Study Area, San Juan County, Utah, 2009. Locations of randomly generated points used to assess habitat conditions in currently, historically, and potential habitat occupied by Gunnison sage-grouse. Occupied habitat is within the boundary of the Conservation Study Area. Unoccupied habitat is located outside of the Conservation Study Area boundary.....65

3.3. Location of vegetation monitoring points and known Gunnison sage-grouse locations within the Conservation Area, San Juan County, Utah, 2009.....71

3.4. Gunnison Sage-grouse (*Centrocercus minimus*) lek counts from San Juan County, Utah. Maximum number of males observed is recorded. Data from Hickman and BLM leks have been combined because of daily movements of males between these 2 leks (SWOG 2008) 73

4.1a-f. Five types of commercially available perch deterrents we evaluated included: a) single and b) paired arrangement of the FireFly™ (P and R Technologies Inc., Portland, OR) hazing deterrent; c) cones (Kaddas Enterprises Inc., Salt Lake City, UT); d) triangles (Kaddas Enterprises Inc., Salt Lake City, UT); e) spikes (Prommel Enterprises Inc., Odenville, AL); and f) control; San Juan County, Utah, 2007-2008 82

4.2a-f. Typical golden eagle perching events documented relative to perch deterrent type on power distribution poles: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL), c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT), d) 2-FireFly™ (P and R Technologies Inc., Portland, OR) arrangement, e) mini zenas, and f) 1-FireFly™ arrangement, San Juan County, Utah, 2007 and 2008.....88

CHAPTER 1

INTRODUCTION

BACKGROUND

In the mid 1970s the Colorado Division of Wildlife began studying sage-grouse (*Centrocercus* spp.) populations located within the state. These studies included the collection of wings from hunted sage-grouse (Young et al. 2000). Biologists noted that primary wings collected from sage-grouse in the Gunnison Basin of Colorado were smaller than those of other populations. These observations prompted further studies on the Gunnison Basin populations. The subsequent studies discovered differences in morphometrics, breeding behavior, plumage and genetics, leading to the reclassification of the grouse species that inhabits the Gunnison Basin in Colorado and southeastern Utah as the Gunnison sage-grouse (*C. minimus*) in 2000 by the American Ornithologists' Union (Young et al. 2000, AOU Checklist Committee 2002, Gunnison Sage-grouse Rangewide Steering Committee 2005).

Species Description

The Gunnison sage-grouse is substantially smaller than the greater sage-grouse (*C.urophasianus*), with shorter tarsus, culmen, and carpal measurements (Schroeder et al. 1999). The average mass of male Gunnison sage-grouse ranges from 1.5-1.82 kg., while the average mass of a male Greater sage-grouse ranges from 2-3 kg. The male Gunnison sage-grouse has considerably larger and thicker filoplumes and shorter rectrices that have more distinct barring. The males of the two species also differ in their strutting displays.

Species Distribution

Gunnison sage-grouse currently occupy 8.5% of their presumed historical range (Schroeder et al. 2004). The Gunnison sage-grouse was thought to have historically occurred in Colorado, Kansas, Oklahoma, New Mexico, Arizona, and Utah before rapid settlement of the west in the 1800s (Young et al. 2000). After a more thorough investigation the species is now believed to have occurred in southwestern Colorado, northwestern New Mexico, northeastern Arizona, and southeastern Utah (Schroeder et al. 2004). The distribution of presumed historic habitat encompassed 46,521 km^2 (21,376 mi^2), but the species is now estimated to have a range of 4,787 km^2 (1,822 mi^2, Schroeder et al. 2004, Fig. 1.1). This decline in the range of the species has been attributed to the loss or conversion of sagebrush (*Artemisia* spp.) to other land uses. The quality of the remaining habitat has been impacted by urbanization, grazing, agriculture and fragmentation (Schroeder et al. 2004). The historic distribution of the species was probably always somewhat patchy, but the patchiness has been greatly exacerbated by habitat loss (Gunnison Sage-grouse Rangewide Steering Committee 2005).

Habitat fragmentation has reduced the Gunnison sage-grouse to seven known populations in Colorado and one population in southeastern Utah (Fig. 1.2). In 2004, the Gunnison sage-grouse population was estimated to be fewer than 3,200 birds; with 2,400 occurring in the Gunnison Basin, Colorado, population (Gunnison Sage-grouse Rangewide Steering Committee 2005). The only known Gunnison sage-grouse population in Utah occurs in San Juan County, Utah, near the town of Monticello. The Monticello, Utah, and the Dove Creek, Colorado, populations are now treated as one

population due to genetic similarities and close geographical proximity (Gunnison Sage-grouse Rangewide Steering Committee 2005).

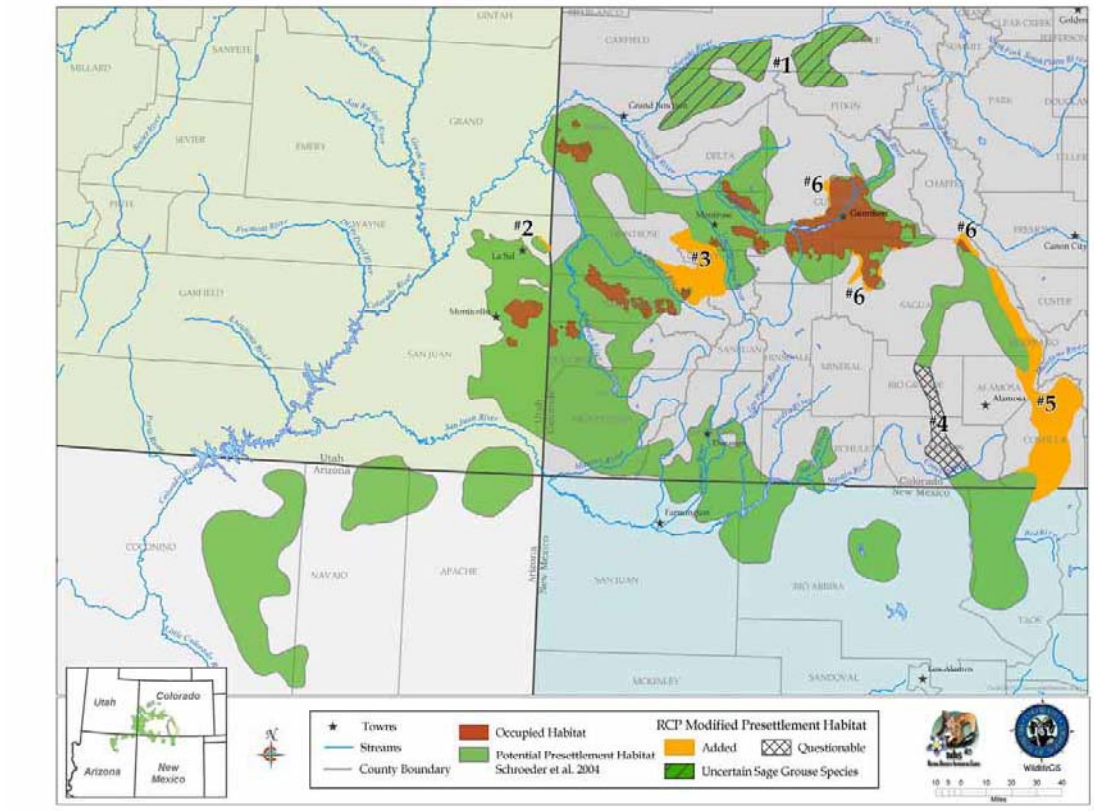


Figure 1.1. Current and historical Gunnison sage-grouse (*Centrocercus minimus*) range (Gunnison Sage-grouse Rangewide Steering Committee 2005).

Species Status and Conservation

Gunnison sage-grouse are considered a species of special concern for management purposes because the rapid decline in the species distribution and abundance

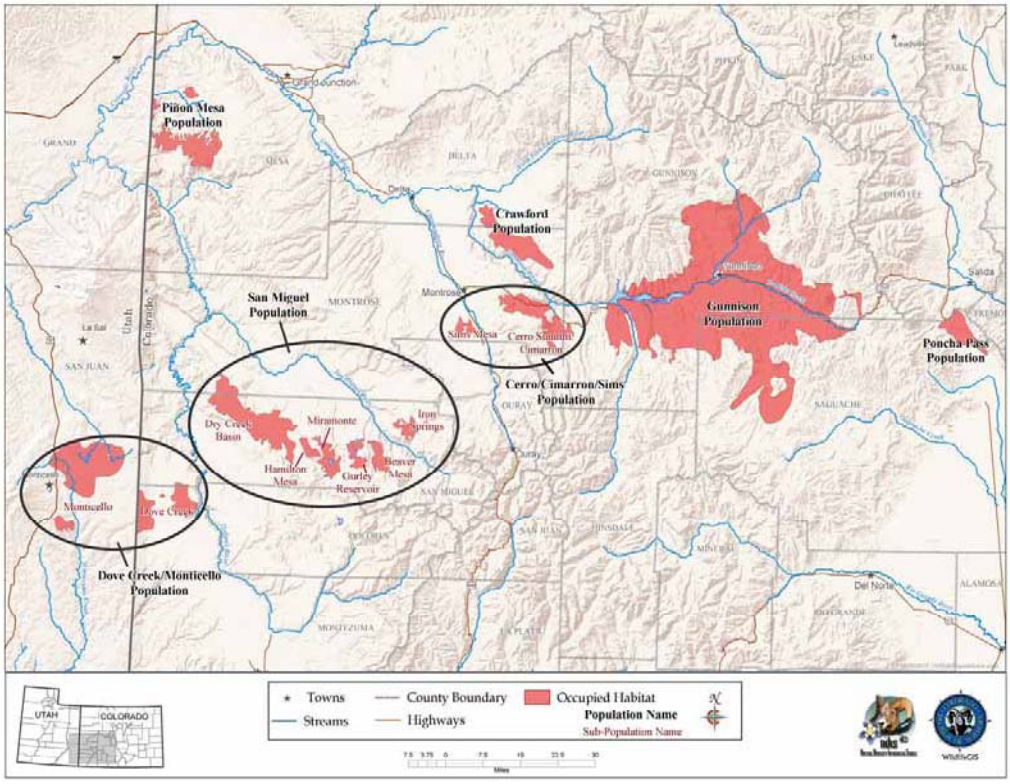


Figure 1.2. Locations of current Gunnison sage-grouse (*Centrocercus minimus*) populations. The discontinuity in occupied habitat at the state line in the Dove Creek/Monticello area is where there is an abrupt change from occupied habitat on the Colorado side to cropland on the Utah side of the border (Gunnison Sage-grouse Rangewide Steering Committee 2005).

has caused the remaining populations to be unusually small and isolated (Oyler-McCance et al. 2005). Identified potential threats to the Gunnison sage-grouse include low genetic diversity, genetic drift from small population sizes, habitat loss, degradation and fragmentation, impacts of drought, predator communities, and the interactions of all these

threats (Gunnison Sage-grouse Rangewide Steering Committee 2005). The greatest threat is the loss, fragmentation, and degradation of sagebrush habitats because of urban development and conversion.

Concern about the small population sizes began in the 1990's. In 1995, before the separation of the sage-grouse into two separate species, the first local working group had formed in the Gunnison Basin of Colorado, with a conservation plan created in 1997 (Gunnison Sage-grouse Rangewide Steering Committee 2005). The formation of local working groups and conservation plans for the other populations soon followed. The San Juan County Gunnison Sage-grouse Local Working Group (SWOG) was formed in 1996 with the purpose of implementing management strategies that would conserve the local population (SWOG 2000). SWOG completed the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP) in 2000. The local working group in Dove Creek, Colorado published a local conservation plan in 1997 with the same purpose.

Continued concerns lead environmental groups to petition the United States Fish and Wildlife Service (USFWS) in January, 2000 to list the Gunnison sage-grouse as endangered (Gunnison Sage-grouse Rangewide Steering Committee 2005). In March, 2000 the USFWS designated the Gunnison sage-grouse as a candidate species for threatened or endangered species status. Under this designation the status of the species was reviewed annually to determine if a listing was still warranted and to determine its listing priority. In 2006 the USFWS ruled to remove the Gunnison sage-grouse from the Candidate Species list.

In 2005, the Gunnison Sage-grouse Rangewide Steering Committee produced the Gunnison Sage-grouse Rangewide Conservation Plan (RCP) to help guide local working groups (Gunnison Sage-grouse Rangewide Steering Committee 2005). In 2006, SWOG merged with the Dove Creek, Colorado, local working group to form the Monticello/Dove Creek Local Working Group (LWG). The merger took place in response to treatment of sage-grouse in Dove Creek and Monticello as one distinct subpopulation in the RCP (Gunnison Sage-grouse Rangewide Steering Committee 2005).

Gunnison Sage-grouse Rangewide Conservation Plan (RCP)

The Gunnison sage-grouse Rangewide Conservation Plan (RCP) was published in 2005 by the Gunnison sage-grouse Rangewide Steering Committee to serve as a guide to aid in the Gunnison sage-grouse conservation efforts (Gunnison sage-grouse Rangewide Steering Committee 2005). The RCP is the first up-to-date and rigorous assessment of the rangewide population and habitat data for the Gunnison sage-grouse. The RCP is intended to supplement local plans and offer a rangewide perspective to help ensure that the cumulative result of conserving local populations is in fact conserving the species. One of the guiding principles of the RCP is to create a plan that will be flexible enough to incorporate Gunnison sage-grouse research findings and successful management practices into conservation actions.

San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP)

The San Juan County Gunnison Sage-grouse Working Group (SWOG) was formed in 1996 to identify and implement community-based conservation strategies to reverse the decline in the Gunnison sage-grouse population in San Juan County, Utah (SWOG 2000). The purpose of SWOG was to develop a conservation plan that could be implemented by state and federal wildlife resource agencies, private landowners, and local governments. Implementation of the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP) helped ensure local ownership of future management and land use decisions, and respect for private property rights.

The SJCCP was initiated to conserve the species by reducing threats, stabilizing populations, and maintaining ecosystems. It was committed to conserving and enhancing Gunnison sage-grouse populations that occurred on privately owned land in the county and to contribute to the economic viability of farms, ranches and the local community. The SJCCP identified conservation strategies that have been and will continue to be implemented by private and public partners to restore Gunnison sage-grouse habitats and populations. The plan's primary purpose was to conserve the species by implementing voluntary conservation actions.

The SJCCP contained two main parts: Habitat Conservation Assessment and Conservation Strategies. The Habitat Conservation Assessment described SWOG's current understanding about the status of the Gunnison sage-grouse distributions, habitat conditions, and factors that may be affecting the county's population. The Conservation Strategies identified goals and objectives, conservation actions, implementation schedules

and responsibilities, evaluation guidelines, and monitoring requirements. The SJCCP was designed to be an adaptive document, capable of being updated with new information, identified issues, and ongoing management and research activities conducted in the county to guide future implementation.

Utah Population Status

The historic range and population size of the Utah population of the Gunnison Sage-grouse is not well documented (Gunnison Sage-grouse Rangewide Steering Committee 2005). Prior to 1968 there is no known written documentation of Gunnison sage-grouse in the Monticello area, but personal accounts of sage-grouse observations from long-time residents indicate that the sage-grouse range extended considerably farther in all directions than the currently occupied area (Fig. 1.3). The Gunnison sage-grouse occur primarily on private land and population declines in the county coincided with land use changes. Lek counts and population monitoring began in 1968. Since 1968, three active leks have been converted from sagebrush to crops or grazed pastures (Gunnison Sage-grouse Rangewide Steering Committee 2005). The number of birds on these leks declined rapidly and the leks were eventually abandoned (Fig. 1.4). In 2003, the population was estimated to be between 100-120 individuals (Gunnison Sage-grouse Rangewide Steering Committee 2005).

Land use in this area changed between 1984 and 1998. These land use changes included declines in non-irrigated agricultural land, black sagebrush (*Artemisia nova*), water areas, pinyon-juniper (*Pinus* spp*., Juniperus* spp.) and big sagebrush (*A. tridentata*), and conversion of land to Conservation Reserve Program (CRP) fields.

In 1997, SWOG designated a Gunnison sage-grouse priority conservation area northeast of the town of Monticello (Fig. 1.5, SWOG 2000). The Conservation Area (CA) contains 1,392,812 ha, 38% (127,170 ha) of which are privately owned. The CA was identified by encompassing historic and current lek sites, potentially suitable sage-grouse habitat, and sage-grouse observations. Within the CA, SWOG identified a Core Conservation Area (CCA) that consists of 136,249 ha, of which 89% (88,420 ha) are privately owned. Within the CCA, a Conservation Study Area (CSA) has been identified. The CSA consists of 24,177 ha, over 93% (22,556 ha) of which is privately owned. The CSA contains the year-round range of the population.

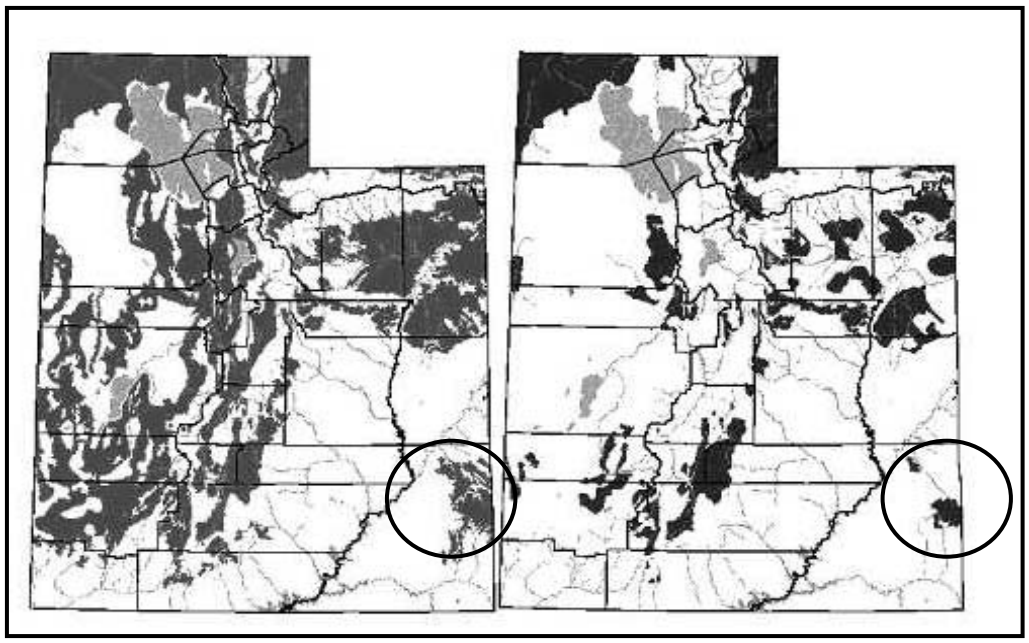


Figure 1.3. Historic (left) and current (right) distribution of Greater sage-grouse (*Centrocercus urophasianus*) and Gunnison sage-grouse (*C. minimus*) in Utah (Beck et al. 2003). Gunnison sage-grouse distributions in San Juan County, Utah are circled.

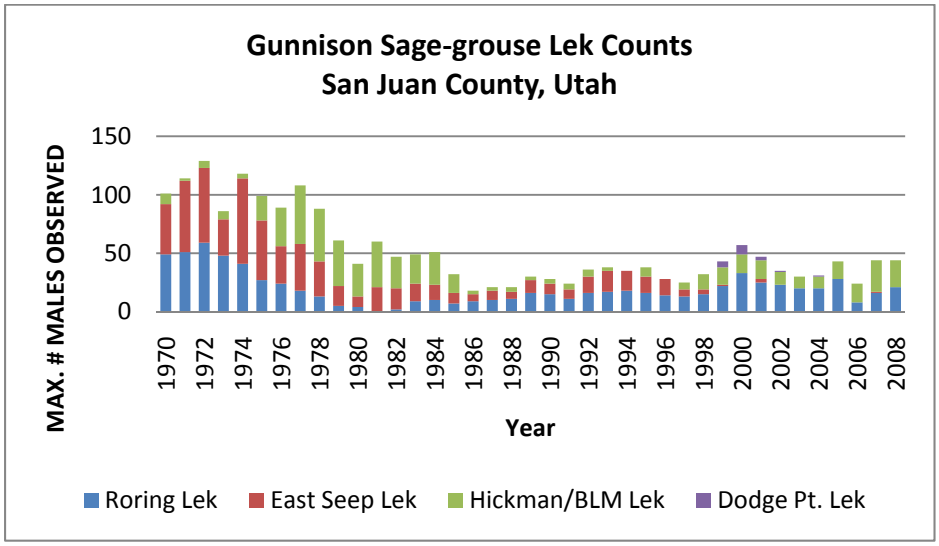


Figure 1.4. Gunnison Sage-grouse (*Centrocercus minimus*) lek counts from San Juan County, Utah. Maximum number of males observed is recorded. Data from Hickman and BLM leks have been combined because of daily movements of males between these two leks (SWOG 2008).

Ecology of the Utah Population

Intensive monitoring of radio-collared Gunnison sage-grouse and their habitats began in 2001 to initiate the process of implementing the SJCCP (SWOG 2003). These studies provided SWOG with information on the basic population ecology and dynamics, habitat use, and the response of the population to management actions. These were the first studies conducted on the Monticello, Utah, population.

Lupis (2005) investigated the movement and habitat use patterns, nesting, brood-rearing and summer habitat use, and factors that might be limiting the San Juan County population in a study conducted from March to September of 2001 and 2002. The objectives of the study were to: 1) Identify and evaluate nesting and brood-rearing habitat

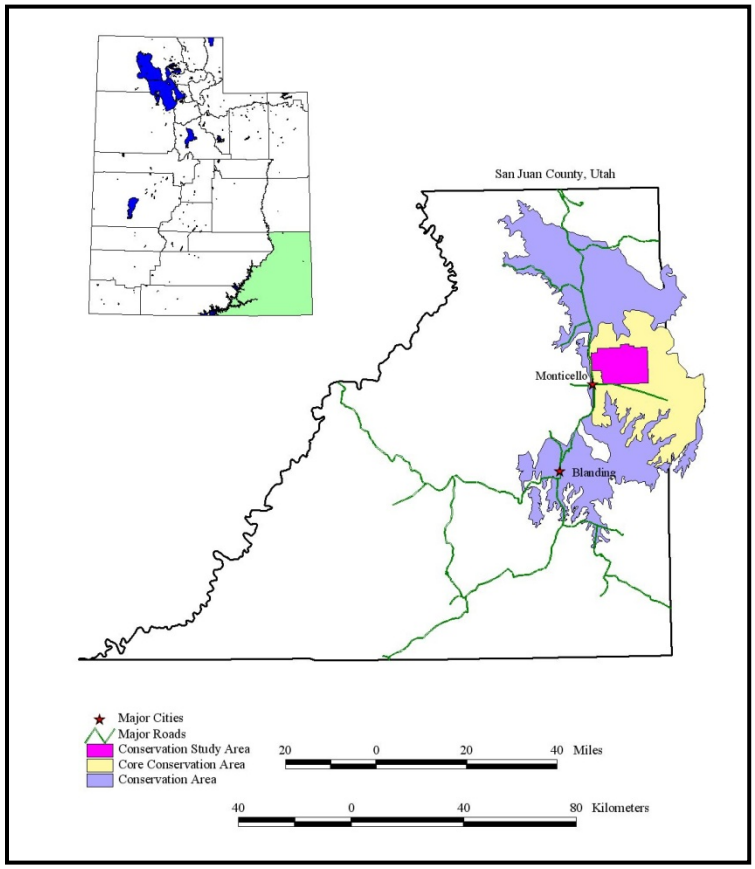


Figure 1.5. Gunnison sage-grouse (*Centrocercus minimus*) Conservation Area, San Juan County, Utah (Lupis 2005).

used by radio-collared hens; 2) Identify and evaluate summer habitat used by radio-collared males and broodless hens; 3) Assess movement patterns, reproductive success, survival, and mortality for radio-collared grouse; and 4) Determine use of CRP lands by Gunnison sage-grouse and their response to management practices. The information gained was compared to that of other Gunnison sage-grouse populations.

Ward (2007) conducted a study from 2002-2004 to determine: 1) reproductive success, survival, and mortalities of Gunnison sage-grouse in San Juan County; 2) nesting

and brood-rearing success for Gunnison sage-grouse hens; 3) winter habitat use of Gunnison sage-grouse; and 4) arthropod abundance and diversity related to vegetative composition at nest (sagebrush) and potential brood-rearing sites (CRP lands) for Gunnison sage-grouse hens.

Nesting. - Three nests, located 0.48 km to 3.3 km from the nearest active lek site, were monitored (Lupis 2005). All nests successfully hatched some eggs between 21-23 May, with clutch sizes ranged from 6-10 eggs. Using background research from other populations in combination with the hatch dates from this study, nest initiation was estimated to occur between 25-27 April, with peak mating occurring between 14-16 April. All nests were laid under sagebrush, with one hen nesting in black sage (*A. nova*) and two nesting in CRP/grassland. The dominant shrub at nest sites was big sagebrush (*A. tridentata*), the dominant grass was crested wheatgrass (*Agropyron cristatum*), and the dominant forb was alfalfa (*Medicago* spp.). The height of the nest bush ranged from 21-22 cm.

The SJCCP identifies the breeding complex as all land within two miles of a known lek site (SWOG 2000). The desired vegetation conditions include a canopy cover of 20-40% big sagebrush with an average height of 40 cm, a 30% minimum grass canopy cover, and a 10% minimum forb canopy cover. From 2000-2001 the mean percentages of vegetation cover types at monitored nest sites included 27.5% shrubs, 6% grass and 0.5% forbs (Lupis 2005, Ward 2007). Reference sites randomly selected in black sagebrush and CRP/grassland cover types were composed of 10.4% shrubs, 34.7% grass and 8.8% forbs. From 2003-2004 the mean percentage of vegetation cover types at

monitored nest sites included 42.9% shrubs, 2.7% grass and 1.4% forbs, compared to reference sites with 36.8% shrubs, 0.7% grass and 0.4% forbs (Ward 2007).

Brood-rearing. - Two radio-collared hens with broods and one uncollared hen with a brood were monitored for approximately 90 days post-hatch (Lupis 2005). One hen fledged two or three chicks (a final count was unattainable), one hen fledged two chicks, and one hen failed to fledge any chicks. The two broods moved a distance of 2.7 km and 3.0 km from the nest site, with home range size ranging from 3.03 km^2 to 3.54 km^2. The hen with no brood had a home range of 12.6 km^2. Broods preferred CRP/grassland and big sagebrush habitat to any other cover type, such as black sage, bare ground, and grazed lands with little vegetation. Brood locations supported more forb cover, and less grass and shrub cover than reference sites.

The SJCCP identifies the need to establish and maintain a canopy cover of 20-40% big sagebrush, 30% minimum grass canopy cover, and a 10% minimum forb canopy cover in brood-rearing areas (SWOG 2000). In 2001, brood location sites consisted of 6.1% shrubs, 14.8% grass and 9.5% forbs with an average height of 18.8 cm (Lupis 2005, Ward 2007). In 2002 the vegetation characteristics of brood locations consisted of 2.8% shrubs, 5.7% grass and 1.7% forbs with an average height of 12.2 cm. The percent cover types for reference sites consisted of 10.4% shrubs, 34.7% grasses, and 8.8% forbs.

From May to August of 2003 and 2004 female Gunnison sage-grouse were monitored to determine nest site selection and nest success (Ward 2007). Vegetation characteristics and arthropod abundance and diversity were collected in sagebrush cover types and compared with random CRP sites. The CRP fields yielded a greater forb and

grass cover than other habitats. Seventy-five percent of the bird habitat use locations and 60% of the total number of arthropods collected were in CRP fields. A larger number of arthropod families were found within CRP fields than other habitats. A higher number of arthropods were collected in 2004 than 2003 possibly because the higher amount of precipitation that year contributed to more vegetation growth. In San Juan County CRP appears to serve as a substitute habitat for arthropod populations in lieu of irrigated pastures, and wheat and bean fields. It now appears to provide critical seasonal use for grouse. Because of this, it has become a conservation priority for continued enrollment and management of current CRP fields and the enrollment of other fields in the program.

Males and Broodless Hens. - Radio-collared males and hens without broods used similar habitats to those utilized by hens with broods described above (Lupis 2005). Males remained within 3.6 km of the lek of capture and selected CRP/grassland and big sagebrush habitats in preference to the other cover types available. Broodless hens selected woodlands, CRP/grasslands and rangelands, and remained within an average of 4.4 km of the lek of capture, but one hen moved a distance of 7.4 km. Birds captured on the Hickman Flat lek were found in mixed-sex flocks of two to eighteen individuals. Birds captured on the Roring lek remained in single-sex flocks of one to sixteen individuals.

Winter. - In the winter of 2002-2003 the Gunnison sage-grouse used black sagebrush and big sagebrush with a canopy cover of 15-25% more than expected based on availability (Ward 2007). In the winter of 2003-2004 black sagebrush and big sagebrush within CRP were selected in greater proportion based on availability. Shrub

height at bird locations ranged from 17.8-91.4 cm. The ideal combination appeared to consist of black sage intermixed with patches of Wyoming big sagebrush. Black sage only occupies 7% of the eastern portion of the area occupied by the population and it was discovered that the majority of the radio-collared birds moved to the eastern side of the study area to winter in the black sage area. The distance traveled between summer and winter habitats for adult grouse ranged from 0.3 to 5.6 km for males, and 2.5 to 8.2 km for females. Average winter home range for males was 2.5 km^2 and 3.0 km^2 for females. Flock sizes were found to be between two and thirty plus individuals.

Suitable winter habitat appears to be limited in the area occupied by the Gunnison sage-grouse population. Because of this, conservation efforts should be directed at preserving and enhancing the remaining black sage patches and establishing additional areas of Wyoming big sagebrush and black sage within CRP fields throughout the study area. The SJCCP calls for the establishment of vegetation conditions on 50% of the areas within the CSA and 25% of the buffer area around the CSA (SWOG 2000). The desired conditions stated within the plan consist of a minimum 15% canopy cover of big sagebrush averaging a height of 30 cm on south and west facing slopes interspersed with small areas of dense big sagebrush with a canopy cover of 40% and an average height of 40 cm. Drainages should support a minimum canopy cover of 30% big sagebrush with an average height of 50 cm.

STUDY PURPOSE

This study addressed three conservation strategies identified in both the RCP and SJCCP. The first conservation strategy addressed was the creation or enhancement of brood-rearing habitats. I attempted to create or enhance brood-rearing habitats using irrigation and dormant season cattle grazing. My objective was to evaluate the effect of irrigation and dormant season cattle grazing of CRP fields and native sagebrush fields on sage-grouse productivity potentials as measured by changes in vegetation composition and structure, arthropod diversity and abundance, and bird use.

The second conservation strategy I addressed was the assessment of vegetation conditions and habitat quality of current and historical Gunnison sage-grouse habitats in Utah. My objective was to collect vegetation data in occupied and potential habitats as identified in the RCP and SJCCP to assess the status of existing and potential Gunnison sage-grouse habitat in the CA. Managers will be able to use this information to quantify the relative contribution of occupied and potential habitats to the overall RCP goals. This information can also be used to update the current SJCCP and the information in the RCP and prioritize conservation efforts.

The RCP and SJCCP also identified the presence of man-made vertical structures such as power poles and fence lines as a threat to Gunnison sage-grouse conservation. Connelly et al (2000) reported that vertical structures in areas occupied by sage-grouse provide raptors and corvids with new perches that could result in increased predation on adults, chicks, and nests. The RCP and SJCCP recommended as a conservation strategy that power poles within areas occupied by Gunnison sage-grouse be fitted with deterrents

to discourage perching by potential sage-grouse avian predators. However, little information was currently available regarding the efficacy of commercially available perch deterrents. To address this management need, I evaluated the effectiveness of five types of perch deterrents in the reduction or prevention of corvid and raptor perching events on poles of a power distribution line with the objective of determining if raptor or corvid use of the distribution line differed by perch deterrent type and/or control.

LITERATURE CITED

AOU Checklist Committee. 2002. Forty-second supplement to the American Ornithologists' Union checklist of North American Birds. The Auk 117: 847-858.

Beck, J.L., D.L. Mitchell, and B.D. Maxfield. 2003. Changes in the distribution and status of sage-grouse in Utah. Western North American Naturalist. 63:203–214.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulleting 28(4): 967-985.

Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.

Lupis, S.G. 2005. Summer ecology of Gunnison Sage-grouse (*Centrocercus minimus*) in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Oyler-McCance, S.J., J. St. John, S.E. Taylor, A.D. Apa, and T.W. Quinn. 2005.

Population genetics of Gunnison Sage-grouse: implications for management. Journal of Wildlife Management 69: 630-637.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2000. Gunnison Sage-grouse Conservation Plan, San Juan County, Utah, USA.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2003. Gunnison Sage-grouse Conservation Plan Update, San Juan County, Utah, USA.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2008. Gunnison Sage-grouse Annual Report, San Juan County, Utah, USA.

Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Pages 1-28 *in* Poole and F. Gill, editors. The birds of North America, No. 425. The Birds of North America, Philadelphia, Pennsylvania, USA.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, MA. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363-376.

Ward, S. 2007. Gunnison sage-grouse winter ecology and arthropod abundance diversity in relation to habitat use in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Young, J.A., C.E Braun, S.J. Oyler-McCance, J.W. Hupp, and T.W. Quinn. 2000. A

new species of sage-grouse (Phasianidae: *Centrocercus*) from southwestern Colorado. Wilson's Bulletin 112: 445-453.

CHAPTER 2

EFFECT OF IRRIGATION AND DORMANT SEASON CATTLE GRAZING ON VEGETATION DIVERSITY AND ARTHROPOD ABUNDANCE IN CONSERVATION RESERVE PROGRAM AND NATIVE SAGEBRUSH IN SAN JUAN COUNTY, UTAH

ABSTRACT Gunnison sage-grouse (*Centrocercus minimus*) populations currently occupy 4,787 km^2 (8.5% of the original range) in Colorado and Utah. Declining populations are characterized by reduced recruitment attributed to breeding habitat (lekking, nesting, and brood-rearing) loss and fragmentation. Increased availability of forbs and arthropods in brood-rearing habitats has been positively associated with survival and recruitment of sage-grouse chicks. Concomitantly, the Gunnison Sage-grouse Rangewide Conservation Plan (RCP) and the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP) identified protection and enhancement of mesic brood-rearing habitats as a priority conservation strategy.

From 2007-2009, I evaluated Gunnison sage-grouse use, vegetation and arthropod responses to irrigation and dormant season cattle grazing on 32 randomly selected 0.1 ha plots, with 12 plots located in agricultural lands enrolled in the Conservation Reserve Program (CRP) and 12 plots in a native sagebrush area. Specifically, I evaluated the role of irrigation and dormant season cattle grazing in creating mesic wet meadow environments and their effect on habitat quality as measured by changes in vegetation structure and composition, arthropod abundance and diversity, and sage-grouse use. Vegetation in the irrigated plots remained greener longer through the growing season

than in the non-irrigated plots, but vegetation diversity did not differ ($p>0.01$). Overall, the CRP plots exhibited greater arthropod abundance and percent cover of perennial grass than the native sagebrush plots, but lower diversity of perennial grasses and abundance and diversity of forbs ($p<0.01$). Crested-wheatgrass (*Agropyron cristatum*) was the dominate vegetation in CRP and may have out-competed native forbs. Dormant season grazing of CRP did not have a positive or negative effect on crested wheatgrass cover. Lastly, I did not detect any increased sage-grouse use of the treatment plots.

The sprinkler irrigation system used in this study allowed quantification of water application rates leaving the nozzle but not actual application rates because of frequent winds that resulted in non-uniform plot coverage and increased evaporation. Thus, creation of mesic areas in brood-rearing habitats may best be accomplished by a system of terraces, ditch plugs or small check dams that retain moisture longer, and by providing flood irrigation. To increase forb and grass diversity in CRP, managers should evaluate the use of mechanical treatments, coupled with spring grazing, and reseeding to mitigate the potential competitive effects of crested wheatgrass.

INTRODUCTION

Connelly et al. (2000) identified several factors contributing to the continued decline of sage-grouse (*Centrocercus* spp.) populations range-wide. Of these, the loss, degradation, and fragmentation of the sagebrush (*Artemisia* spp.) ecosystem remain paramount. As sagebrush obligates, sage-grouse require this habitat type to complete their life cycle. The structure and composition of plant communities within sagebrush

ecosystems influence sage-grouse nesting, breeding, brood-rearing, fall, and winter habitat selection.

Gunnison sage-grouse (*C. minimus*) currently occupy 4,787 km^2 (8.5% of their original range) in Colorado and Utah. The Gunnison Sage-grouse Rangewide Conservation Plan (RCP) and the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP) recommend management strategies to conserve the species by restoring impacted habitats (SWOG 2000, GSRSC 2005). Both plans identified the lack of brood-rearing habitat as limiting sage-grouse productivity and recommended the creation of mesic areas for broods as a priority conservation strategy.

Sage-grouse Brood-rearing Habitats

Good brood-rearing habitat includes areas with an abundant diversity of forbs and insects high in calcium, phosphorus and protein, and the availability of herbaceous plant species during the late-growing season (Peterson 1970, Wallestad 1971, Klott and Lindzey 1990, Johnson and Boyce 1990, Sveum et al. 1998, Connelly et al. 2000, Crawford et al. 2004). The quality of brood-rearing habitats changes as summer progresses and food availability shifts. The habitats tend to become more xeric resulting in desiccation of forbs. Increased sage-grouse brood use of wet meadow areas has been related to the amount of desiccation occurring.

Wallestad (1971) documented the summer movements and habitats used by broods in central Montana. He observed that hens with broods occupied areas characterized by mixed sagebrush and open areas exhibiting succulent forbs and clumps of tall sagebrush for hiding and roosting cover. As the season progressed into late August

and early September the broods shifted to areas where sagebrush was more common and dense. He concluded that large tracts of dense sagebrush appeared to have little value as sage-grouse brood habitat, even though it is essential as winter habitat. Peterson (1970) and Klott and Lindzey (1990) reported that an important component of juvenile sage-grouse habitat appears to be an abundance and diversity of forbs with sagebrush cover <20%. Broods used areas with less shrub cover than what was average for that habitat.

Crawford et al. (2004) suggested that the availability of forbs and invertebrates is positively associated with survival and recruitment of chicks. Johnson and Boyce (1990) conducted a study on captive-reared sage-grouse chicks and the influence of insect reduction in their diet on survival. They reported a correlation between the quantity of insects in the diet and chick survival and growth. Chicks less than 21 days old needed insects to develop and survive. All chicks hatched in captivity that were not given insects died between the ages of 4 and 10 days. Insects decreased in the diets of chicks >21 days of age but were still required for optimum development.

The diets of broods in Oregon included 34 genera of forbs and 41 families of invertebrates (Drut et al. 1994). Klebenow and Gray (1968) recorded weekly diet selection data for age classes of sage-grouse chicks from hatch until brood break up at eight to ten weeks of age. During the first week insects were predominant, composing 52% of the total diet. After the first week, insects decreased in importance but were still part of the diet. As insects decreased, forbs became the most important food source for chicks. At four weeks, as plants began to dry, sagebrush appeared in the diet in small

amounts, progressively increasing as the season progressed and the availability of forbs decreased. Similar findings were also reported by Peterson (1970).

Drut et al. (1994) quantified the importance of forbs and invertebrates in sage-grouse productivity in Oregon. They reported higher productivity in a population where 80% of the dietary mass in chicks diets consisted of forbs and arthropods compared to another study area where chick diets consisted of 65% sagebrush. Sveum et al. (1998) suggested a brood that needs a larger home range due to limited availability of forbs may also have a lower survival rate than a brood using a smaller area exhibiting a greater abundance in forbs.

Gunnison Sage-grouse Brood-Rearing Habitat in Utah

In 1997, the San Juan County Gunnison Sage-grouse Local Working Group (SWOG) designated an area northeast of the town of Monticello, Utah, as a sage-grouse priority conservation area (SWOG 2000). The Conservation Area (CA) consisted of 1,392,812 ha, 38% (127,170 ha) of which is privately owned. The CA was identified by encompassing historic and current lek sites, potentially suitable sage-grouse habitat, and sage-grouse observations. Within the CA, SWOG identified a Core Conservation Area (CCA) that consisted of 136,249 ha, of which 89% (88,420 ha) is privately owned. Within the CCA, a Conservation Study Area (CSA) was identified. The CSA consisted of 24,177 ha, over 93% (22,556 ha) of which is privately owned. The CSA contains the year round range of the Utah population.

The SJCCP stated that the desired brood-rearing habitat conditions should include a canopy cover of 20-40% sagebrush with an average height of 40 cm, a minimum of 30% grass canopy cover, and a minimum of 10% forb canopy cover. The SJCCP further recommended that the height of the vegetation in wet meadow areas is to be greater than 10 cm between 15 June and 31 July on over 75% of the area considered to be brood-rearing habitat.

The Farm Program and Sage-grouse Conservation

Because over 90% percent of the habitat occupied by Gunnison sage-grouse in San Juan County is privately owned, the implementation of the Conservation Reserve Program (CRP) under the Food Security Act of 1985 was recognized by SWOG as a major species conservation action. The CRP is a voluntary program that provided financial incentives to encourage private landowners to retire cropland from agricultural production by establishing an approved permanent vegetation cover. During the period of the contract, the land could not be cultivated to produce an agricultural commodity. Haying and grazing were allowed on a case-by-case basis to mitigate the effects of drought on local livestock producers. The only techniques allowed to manage CRP fields are burning, spraying for noxious weeds, and mowing.

The Farm Security and Rural Investment Act of 2002 (Farm Bill) reauthorized the Environmental Quality Incentives Program (EQIP) to provide a voluntary conservation program for farmers and ranchers that promotes agricultural production and environmental quality. This program offered financial and technical help to assist eligible participants to install or implement structural and management practices on

eligible agricultural land. This study used management practices within EQIP that could be employed by landowners in the CCA to enhance sage-grouse brood-rearing habitat through the creation of mesic environments. These environments could potentially increase forb cover and arthropod diversity in existing CRP fields and provide important seasonal habitats for sage-grouse broods.

Land Use Changes in San Juan County and Gunnison Sage-grouse

Gunnison sage-grouse population declines in San Juan County have coincided with land use changes. The population was at its highest in the 1970s and 1980s (SWOG 2003, Lupis 2005). During this period, the primary agricultural crops in the county were winter wheat (*Triticum* spp.) and dryland alfalfa (*Medicago* spp.). Many growers did not use herbicides or insecticides because of the slim profit margin in growing these crops (J. Keyes, Utah State University Extension, personal communication). These practices may have resulted in a greater arthropod abundance as a result of increased green vegetation and forb availability. During this period landowners also frequently reported observing flocks of grouse in their fields during harvest and post-harvest periods.

In the past, many landowners in San Juan County did not have automatic control valves on wells used to fill livestock water tanks (SWOG 2000). This would cause tanks to overflow, inadvertently creating mosaics of ephemeral wet meadow or mesic habitats below the tanks. These overflow areas were not grazed by livestock until late fall when the herds were moved to winter pasture. Landowners reported these holding corrals continually produced more forage, greened-up earlier, stayed greener longer than

adjacent areas, and often supported sage-grouse broods. The SWOG believed this activity enhanced Gunnison sage-grouse productivity (SWOG 2000). But with more efficient watering devices the seasonal wet meadows disappeared. The SWOG believed that the loss of these wet meadow or mesic sites in brood-rearing areas could be a potential reason for low sage-grouse numbers and low recruitment because the quality and quantity of herbaceous cover has been reduced.

CRP and Sage-grouse

One of the most comprehensive land use changes to occur in the county was the conversion of thousands of hectares of cropland to CRP. Because of drought conditions many of these CRP fields had to be reseeded, and thus were devoid of vegetation for almost two years (G. Wallace, Utah Division of Wildlife Resources, personal communication). In the two years post-CRP signup the number of males counted on lek sites decreased by 50%.

In 1997 the habitat for the San Juan County population was designated as a priority conservation area for the species (Lupis 2005). This designation increased the amount of land that could qualify as CRP, adding an additional 150 km^2 of land enrolled in the program (Fig. 2.1). However, based on lek counts, the San Juan County population is at a historic low with a 2004 population estimate of 155 to 174 birds (SWOG 2005). Research suggested that CRP habitats appear to provide the greatest arthropod abundance

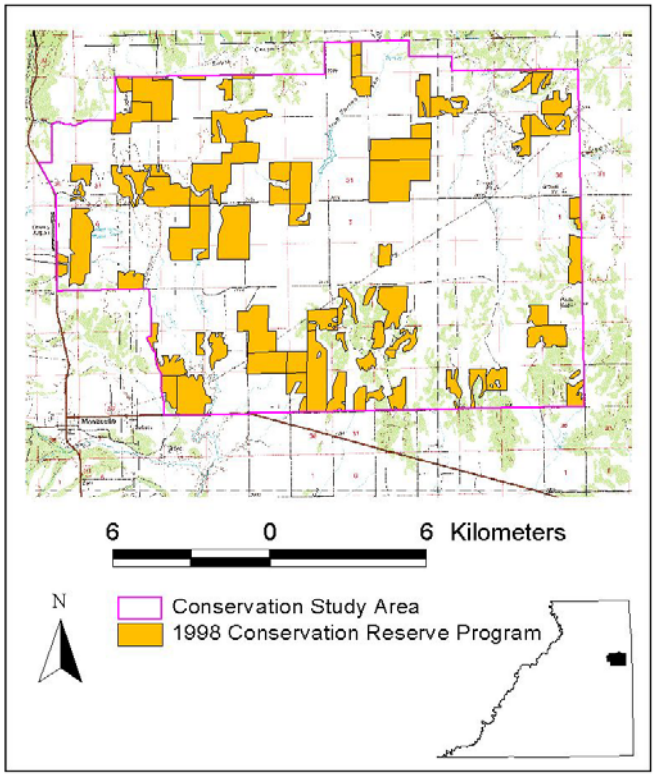


Figure 2.1. Agricultural lands enrolled in the Conservation Reserve Program under the conservation priority initiative in the Conservation Study Area, San Juan County, Utah (Lupis 2005).

(Lupis 2005, Ward 2006). These CRP fields are also preferred over other cover types during the brood-rearing period (Lupis et al. 2006).

Beginning in late 2001, San Juan County experienced a major drought. In response to drought conditions, the FSA opened CRP for late season grazing. Grazing was allowed on several CRP fields in the CSA. Lupis (2005) investigated the effects of domestic livestock grazing of the CRP fields on the movement patterns of Gunnison sage-grouse.

Three males, 2 broodless hens, and 1 hen with a brood were monitored before, during, and after grazing. Males avoided the grazed CRP fields during grazing and did not return after the livestock were removed. Two of the males were located within a CRP field during grazing 15-20% of the time, and 1 male was recorded in a grazed field 40% of the time. Broodless hens also avoided CRP fields during grazing to varying degrees. One hen was in a CRP field during grazing 78% of the time, 1 female 12.8% of the time and returned twice after livestock was removed, and 1 hen was never located within a CRP field during or after grazing. The monitored brood remained within the CRP field during grazing and successfully recruited 2 chicks into the fall population.

STUDY PURPOSE

This study addressed the RCP and SJCCP conservation strategy of evaluating methods to create or enhance brood-rearing habitats. The specific objectives of my research were to evaluate; 1) the role of irrigation in CRP and native sagebrush on sage-grouse habitat potentials as measured by changes in vegetation composition and structure, arthropod diversity and abundance, and bird use; and 2) the role of dormant season cattle grazing on these same potentials.

STUDY AREA

The study was conducted in San Juan County, located in the extreme southeastern corner of Utah (Fig. 2.2). The county is bordered by the Colorado River to the north and west, Arizona to the south, and Colorado to the east. The CSA is part of the Colorado Plateau Province and sits on the extensive Sage Plains tableland on the northeast side of

the Abajo Mountains with an elevation between 2,042 m and 2,133 m (Olsen et al. 1962). The surface of the plateau consists of undulating to rolling, low hills of eolian deposits of variable thickness derived from sandstone over colluvium and/or residuum weathered from sandstone. The area is characterized by large grass pastures and agricultural fields interspersed with fragmented patches of Wyoming big sagebrush (*A. tridentate* spp. *wyomingensis*) and black sagebrush (*A. nova*). There are no perennial water sources on the plateau. The CSA consists of 95% privately owned land, most of which is currently enrolled in CRP. The remaining privately owned lands are used as rangeland pastures for cattle grazing or dryland farming.

Long term (1902-2009) precipitation and temperature for the CSA was summarized from local weather station data archived by the Utah Climate Center, Logan, Utah. Precipitation and temperature measurements for the study period (2007-2009) are summarized from data recorded on a portable weather station. The long-term average annual precipitation (1902-2009) in the study area was 39.55 cm, with most arriving from July to October in the form of rain. The mean annual high and low temperatures on the study area were 35.9° C and -21.2° C, respectively. From 2007-2009 the average annual precipitation on the study area was 30.23 cm, with average annual high and low temperatures of 37.5 ° C and -18.3 ° C, respectively.

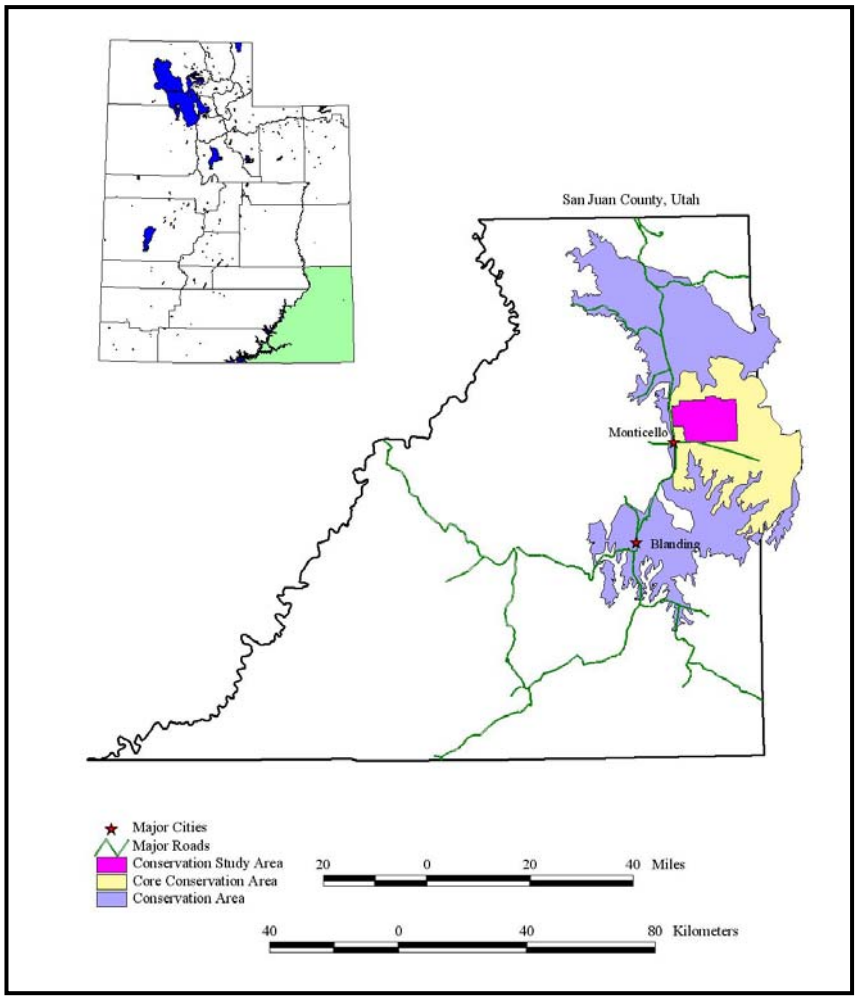


Figure 2.2. Gunnison Sage-grouse Conservation Area, San Juan County, Utah (Lupis 2005).

The CSA is relatively flat with elevations ranging from 2,065-2,149 m. The CSA is a mosaic of habitat types dominated by CRP/grassland and sagebrush cover types (SWOG 2000). The original seed mixture for the CRP fields and the plant species recorded within the CRP and sagebrush plots during this study can be found in

Appendices A and B, respectively. The dominant forb species recorded in the sagebrush plots were scaly globemallow (*Sphaeralcea leptophylla*), sulphur buckwheat (*Eriogonum umbellatum*), hairy golden aster (*Heterotheca villosa*), and cryptantha (*Cryptantha* spp.). Few plants from the original CRP seed mixture were found in the CRP plots. The dominant species in the CRP plots was crested wheatgrass (*Agropyron cristatum*) with occasional patches of Wyoming big sagebrush and rubber rabbitbrush (*Chrysothamnus nauseosus*). Dominant forb species within the CRP plots were Russian knapweed (*Centaurea repens*), African mustard (*Malcomia africana*), and Russian thistle (*Salsola pestifer*). Forbs within Wyoming big sagebrush patches in CRP plots were the same as those found in the sagebrush plots. Cheatgrass (*Bromus tectorum*) was present in both CRP and native sagebrush plots.

METHODS

Experimental Design

I identified one study site in a native sagebrush area and one study site in a CRP field, both sites within the CSA. I identified 16 0.1 ha plots in each study site. I arranged the plots in an experimental randomized block design that controlled for differences in vegetation and landscape topography that could affect the vegetation present at each plot. Each plot was considered a separate experimental unit. At each site, the plots were arranged in 4 blocks, with each block consisting of 4 plots (Fig. 2.3). Within a block, each plot was randomly assigned to one of the 3 irrigation treatments or control. Half of each plot was grazed by cattle. Vegetation transects and arthropod trapping grids were

established in both halves of each plot to measure the effects of irrigation and irrigation combined with grazing. This layout resulted in four replications of each irrigation and grazing treatment and control in each habitat.

Irrigation

I evaluated 3 irrigation treatments base on application rates: once a week, every 2 weeks and every 3 weeks. Plots receiving no water served as reference or control sites. Plots were randomly assigned to each irrigation treatment or control within each block. Three groundwater wells in close proximity to the identified treatment plots were used to distribute water to each plot for irrigation. Treatment plots were irrigated with a Rain Bird sprinkler model 65PJ™ with a 30 meter spraying radius (Rain Bird Corporation, Azusa, CA). The treatment and control plots were established in the summer of 2007. Given that there were site-specific differences, we conducted tests before the study began to standardize the capacity of the pumps at each treatment plot. During this period I measured the amount of water distributed on each plot by time. These experiments allowed us to establish a standard rate of flow. Irrigation of the plots began in May 2007 and continued to the end of July. This time period coincided with peak nesting and brood-rearing periods (Lupis 2005, Ward 2006).

All plots were irrigated for an 8-hour period. Due to strong afternoon winds, the irrigation periods occurred in the early morning and evening. Each plot assigned to an irrigation treatment received 1.4 cm of water each irrigation period, the equivalent of the

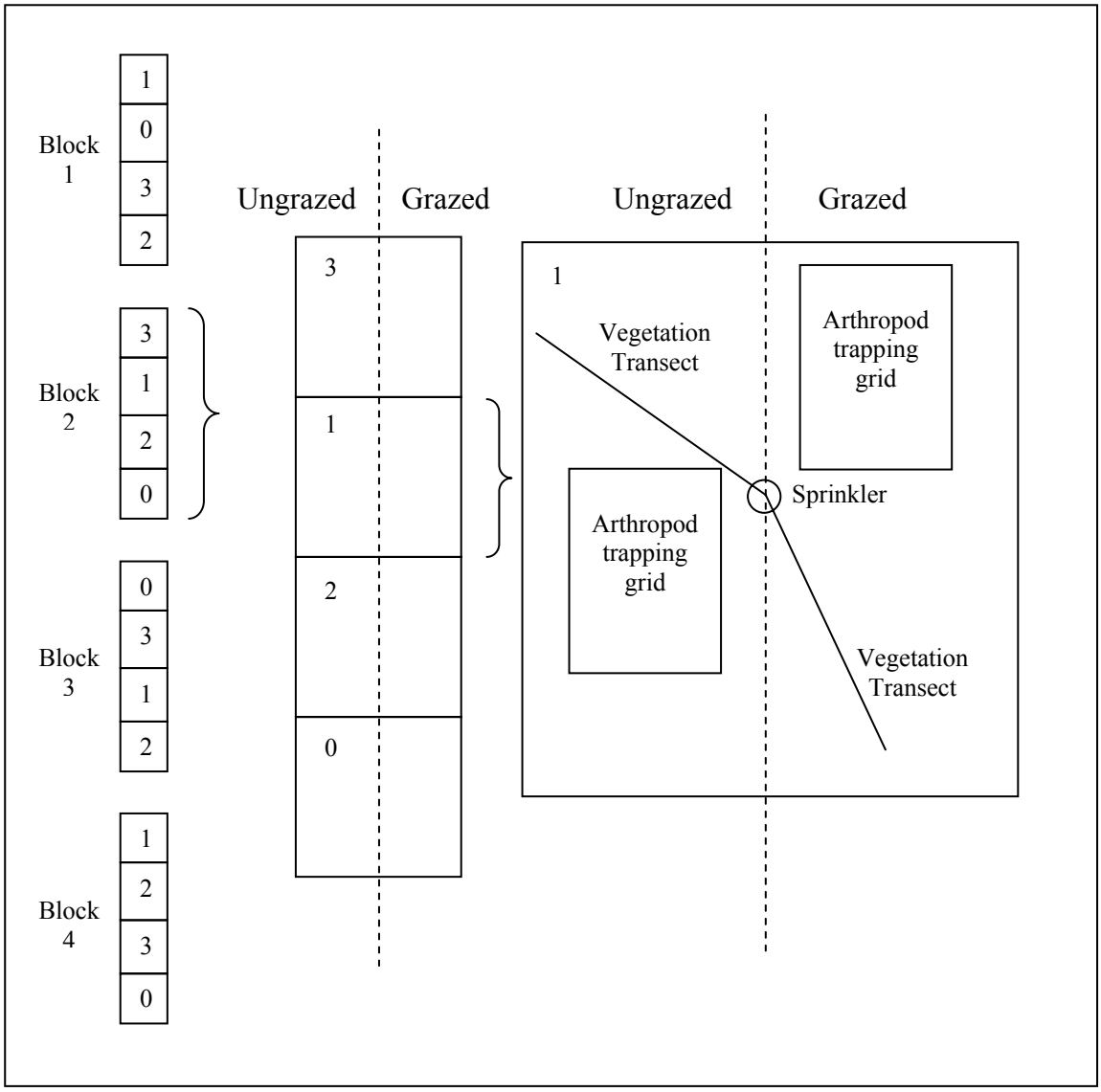


Figure 2.3. Experimental design schematic showing the layout of 4 blocks each containing 3 plots randomly assigned to watering treatments (once a week, every 2 weeks, every 3 weeks) and 1 control (no water) plot, ungrazed and grazed treatments, and location of arthropod trapping grid, vegetation transects, and rain-bird sprinkler. Each 4 block layout occurs within the Conservation Reserve Program and native sagebrush study sites. San Juan County, Utah, 2007-2009.

long term average precipitation this area receives in the months of May, June, and July. Within both CRP and sagebrush sites, the plots that were irrigated weekly over the 7-week period received the equivalent of an additional 10.2 cm of water as measured on test gauges. The plots that were irrigated every two weeks or 4 times over the 7-week period received the equivalent of 5.1 cm of additional water. The plots irrigated every three weeks or 3 times over the 7-week period received the equivalent of 3.8 cm of additional water. The irrigation occurred in May-July of 2007, 2008, and 2009.

Vegetation Monitoring

I used the GSRSC Structural Vegetation Collection Guidelines (SVCG) to measure vegetation parameters (GSRSC 2007). At each site, each treatment and control plot contained one 30-meter vegetation transect. Transects were permanently marked with t-posts with the same transects used in consecutive years. Percent canopy cover of grasses, forbs, and shrubs was visually estimated by placing a Daubenmire frame every 3 m along each 30-m transect (Daubenmire 1959). The SVCG identified six cover classes based on the standardized Daubenmire method. The Daubenmire method lumped too much vegetation into the 5-25% class for the Gunnison sage-grouse vegetation variables, so it was into 2 cover classes. The canopy cover classes used in this study were: 0-5%, 5-15%, 15-25%, 25-50%, 50-75%, and 75-100% (GSRSC 2007).

One height measurement of sagebrush, forb, annual grass, and perennial grass was taken at each Daubenmire frame by selecting the plant closest to the lower left hand corner of the frame. If sagebrush was not found within the frame then the closest sagebrush within 10 m of the frame was used. If no sage was within 10 m of the frame it

was marked as not present. Only forbs and grasses within the frame were used to measure height. If no forb or grass was within the frame the plant group was marked as not being present. Height and percent cover of grasses, forbs and shrubs was measured in early June and again the last week of July.

Vegetation was clipped and weighed to measure the forage production of each plot using a 0.5m x 1m frame. All vegetation within the frame was clipped, stored in paper bags, dried, and weighed. The vegetation was separated into the categories perennial grasses, annual grasses, and forbs. Vegetation was clipped along a 30 m transect radiating from the center sprinkler. Frames were placed every 3 m, resulting in 10 frames. A different transect was used each year to prevent clipping the same location more than once. The clipping transect did not overlap the permanent vegetation monitoring transect. Forage production was measured the last week of July.

Any uncertainties in identification of a plant species were documented with photos and pressings. The same survey method and transect lines were used during the collection of data in 2007, 2008, and 2009 to evaluate the effectiveness of treatment plots in increasing grass and forb abundance and diversity.

Arthropod Surveys

Terrestrial arthropods were sampled by using pitfall traps arranged in a pattern that allowed capture data to be used with DISTANCE software to estimate density of total arthropods and of individual taxa (Buckland et al. 2001, Lukacs et al. 2004, Graham et al. 2008). Pitfall traps in each plot were arranged to meet the assumptions of DISTANCE sampling, which are that all invertebrates on the center line are detected and

that distances from the center line are accurately measured. Sixty pitfall traps were used at each plot in the arrangement shown in Fig. 2.4. This pattern was generated by using WebSim to simulate a hazard-rate model of invertebrate captures that resulted in estimates with small confidence intervals, and matched trapping results in a pilot study of invertebrate pitfall trapping in Colorado (Lukacs 2001, 2002; Graham et al. 2008).

Pitfall traps were placed by carefully measuring and marking correct locations with flags, then digging in the traps. Pitfall traps were constructed as described by New (1998). For each trap, a 1.5-liter plastic jar was buried below ground level and a 500-mL cup containing 125 mL of soapy water was placed in the cup (Graham et al. 2008). A 15-cm diameter funnel was placed over the jar, centered over the cup, with the top of the funnel at ground level. Each water treatment and grazing treatment plot in each of the sagebrush and CRP habitats contained a pitfall trapping arrangement with 60 traps. I sampled in early June, during the estimated first week after hatch for Gunnison sage-grouse nests in San Juan County, Utah (Lupis 2005, Ward 2006). The traps were opened in sequence and remained open for three days during a 7-day period. When closed, each trap was poured into a 150 mL sample container with the remaining space filled with 91% isopropyl alcohol to assure the sample was stored in a 70% isopropyl alcohol and water solution. Labels affixed to the outside of the sample containers recorded habitat, plot number, treatment, date, and trap number. Samples were stored at room temperature once they were returned to the lab.

In the lab, each sample was washed through a 0.5-mm mesh net (Graham et al. 2008). Everything remaining in the net was placed in a Petri dish. Arthropods were

sorted to order. Taxa were identified following Triplehorn and Johnson (2005), and I followed the taxonomic nomenclature of this source. I collected 3,840 total samples each year in 2007, 2008, and 2009. Because of logistical constraints only 2,240 samples were sorted for each year resulting in 35 traps sorted for each trapping arrangement.

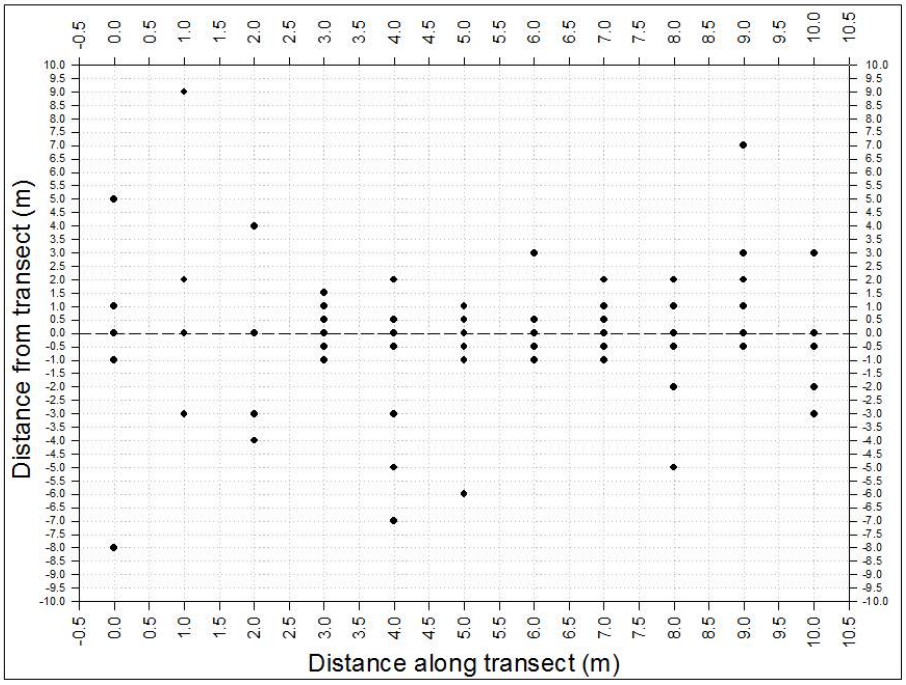


Figure 2.4. Arrangement of pitfall traps at each terrestrial arthropod sampling plot of the study, San Juan County, Utah, 2007-2009 (Graham et al. 2008).

Sage-grouse Pellet Counts

Pellet counts were used to survey sage-grouse use of the treatment and control sites in each habitat (Dahlgren 2005). I established 20 transects two meters apart in each plot. Information collected included pellet type (cecal or regular pellet) and number of

pellets or cecal droppings per cluster. Roost piles were counted separately and equaled one cluster occurrence. Once a pellet was counted it was removed from the site to prevent double counting.

Dormant Season Cattle Grazing

Both CRP and sagebrush plots were grazed in November of 2006, 2007, and 2008. Utilization was measured using a paired-plot design. Utilization cages were randomly placed on the grazed portion of each plot, resulting in 32 cages (USDI-BLM 1996). After grazing, forage within each cage was clipped and weighed. A random uncaged plot was identified on the grazed side of the plot and forage within this plot was also clipped and weighed. The difference between the 2 weights equaled the amount of forage consumed. Random plots were also identified on the ungrazed sides of each site and forage was clipped and weighed to determine the amount of forage production. Annually, 60% utilization was achieved each fall grazing occurred.

DATA ANALYSIS

I used a 3-way factorial split-split plot design with whole plots arranged in randomized complete blocks with repeated measures to analyze habitat metrics. The whole block unit included 4 plots, one of each 3 irrigation treatments and a control. The whole block factor was whether the plot was CRP or sagebrush. The split plot unit was the individual plot. The split plot factor was the irrigation assignment. The split-split plot unit was half of each plot. The split-split plot factor was whether the half was grazed

or un-grazed. The repeated measure unit was the individual plot. The repeated measure factor was the month the vegetation was measured (June or July).

I addressed the question: Did the vegetation and arthropod communities change in relation to water and grazing treatments in CRP and sagebrush plots in 2007, 2008, and 2009? The model I used compared the means among treatments and controls for the percent cover, height and forage production of perennial grasses, annual grasses, forbs and sagebrush, and arthropods observed in 2007, 2008, and 2009. I used a mixed model with an arcsine-square root scale (SAS Institute, Cary, NC). In essence, the statistical model was three-way in a randomized spatial block design, with plots grouped into spatial blocks to control for spatial heterogeneity in the landscape. Data analyses were conducted using the Mixed Procedure in SAS/STAT for Windows Version 9.1.3 (SAS Institute, Cary, NC).

RESULTS

Vegetation and arthropod responses to irrigation and grazing treatments are presented in a series of Tables in Appendix 3.

Vegetation Response

Vegetation cover results for 2007 are presented in Table A.3.1. Annual grass cover differed (p=<0.01) when analyzed by time, with more cover in June than July. When comparing habitat by time there was a difference (p=<0.01) between habitats. The CRP plots had visibly more cheatgrass than the sagebrush plots, but there was no difference between months within CRP over time with June cover of 5.0 % (SE=2.8) and

July having 4.9 % (SE=2.8). There was a slight difference over time within the sagebrush plots with an annual grass cover of 1.8% in June (SE=1.8) and 0.7 % in July (SE=1.3). Cover of forbs differed when analyzed by time (p=<0.01) with a greater cover of forbs in June (3.3 %, SE=0.7) than in July (0.8 %, SE=0.3). Forb cover also differed when analyzed by habitat and time (p=<0.01) with a greater cover of forbs in June than in July in both habitats. The sagebrush plots had a greater cover of forbs than CRP in both June (5.4 %, SE=1.2) and July (0.8 %, SE=0.7). The CRP plots had a forb cover of 1.7 % (SE=0.7) in June and 0.6 % (SE=0.4) in July. Cover of Wyoming big sagebrush differed by habitats (p=<0.01) with CRP plots having a cover of 0.2 % (SE=0.3) and a cover of 13.3 % in sagebrush plots (SE=2.0).

Vegetation cover results for 2008 are presented in Table A.3.2. Perennial grass cover was greater in the CRP plots (32.7 %, SE=3.7) than in the sagebrush plots (17.1 %, SE=3.0) (p=0.02). When analyzed by time, annual grass had a greater cover in June (6.3 %, SE=2.9) than in July (3.1 %, SE=2.2) (p=<0.01). Forb cover differed when analyzing habitat (p=<0.01) and habitat by time (p=<0.01) with more forb cover in the sagebrush plots (4.4 %, SE 0.8) than the CRP plots (0.2 %, SE=0.2) and a greater forb cover in the sagebrush plots in June 5.8 % (SE=1.0) than in July 3.2 % (SE=0.8). But within the CRP plots there was little difference between the June (0.2 %, SE=0.2) and July (0.3 %, SE=0.3) forb cover. When analyzed by habitat, Wyoming big sagebrush cover was greater in the sagebrush plots (9.6 %, SE=1.3) than the CRP plots (0.1 %, SE=0.2) (p=<0.01).

Vegetation cover results for 2009 are presented in Table A.3.3. Perennial grass cover was greater in the CRP (32.7 %, SE=3.7) than the sagebrush plots (17.1 %, SE=3.0) (p=0.02). When analyzed by time, annual grass had a greater cover in July (6.3 %, SE=2.9) than in June (3.1 %, SE=2.2) (p=<0.01). Forbs had a greater cover in the sagebrush (4.4 %, SE=0.8) than the CRP plots (0.2 %, SE=0.2) when analyzed by habitat (p=<0.01). When analyzing habitat by time forbs had a greater cover in the sagebrush plots in June (5.8 %, SE=1.0) than July (3.2 %, SE=0.8), and greater cover than the CRP plots in both months. Wyoming big sagebrush cover was greater in sagebrush (9.6 %, SE=1.3) than CRP plots (0.1 %, SE=0.2) (p=<0.01).

Vegetation height results for 2007 are presented in Table A.3.4. Perennial grass height differed by time (p=<0.01) and habitat (p=<0.01). Perennial grass was taller in June (13.2 cm, SE=1.1) than in July (9.0 cm, SE=0.9) and was taller in the CRP plots (16.4 cm, SE=1.4) than in the sagebrush plots (6.6 cm, SE=1.0). Annual grass was taller in June (4.0 cm, SE=0.5) than in July (2.3 cm, SE=1.2) (p=0.01). Forbs were taller in June (4.0 cm, SE=0.7) than in July (1.3 cm, SE=0.4) (p=<0.01). Wyoming big sagebrush was taller in the sagebrush plots (4.2 cm, SE=4.1) than in the CRP plots (3.6 cm, SE=1.7) (p=<0.01).

Vegetation height results for 2008 are presented in Table A.3.5. Perennial grass was taller in the CRP (24.7 cm, SE=2.5) than in the sagebrush plots (13.5 cm, SE=2.0) (p=0.01). Perennial grass was taller in the CRP plots that were not grazed (27.7 cm, SE=3.0) than in the CRP plots that were grazed (21.9 cm, SE=2.8) (p=0.02). Perennial grass taller in both habitats in July (21.2 cm, SE=1.7) than in June (16.5 cm, SE=1.6)

(p=<0.01). Annual grass was taller in June (3.6 cm, SE=1.2) than in July (2.0 cm, SE=0.9) (p=<0.01). Forbs were taller in the sagebrush plots (3.8 cm, SE=0.5) than in the CRP plots (0.4 cm, SE=0.2) (p=<0.01). Wyoming big sagebrush was taller in the sagebrush plots (43.1 cm, SE=5.0) than in the CRP plots (4.0 cm, SE=2.2) (p=<0.01) and was taller in June (21.5 cm, SE=3.0) than in July (17.9 cm, SE=3.0) (p=<0.01).

Vegetation height results for 2009 are presented in Table A.3.6. Perennial grass was taller in CRP (24.7 cm, SE=2.5) than sagebrush plots (13.5 cm, SE=2.0) (p=0.012) and was taller in July (21.2 cm, SE=1.7) than in June (21.2 cm, SE=1.6) (p=<0.01). Annual grass was taller in June (3.6 cm, SE=1.2) than in July (2.0 cm, SE=0.9) (p=<0.01). Forbs were taller in sagebrush plots (3.8 cm, SE= 0.5) than the CRP plots (0.4 cm, SE=0.2) (p= <0.01). Wyoming big sagebrush was taller in the sagebrush (43.1 cm, SE=5.0) than the CRP plots (4.0 cm, SE=2.2) (p=<0.01) and was taller in July (21.5 cm, SE=3.0) than in June (17.9 cm, SE=2.8) (p=<0.01).

Forage production results for 2007 are presented in Table A.3.7. Annual grass forage production differed (p=<0.01) when I compared habitat by water treatment by grazing treatment. The results suggested that in both habitats annual grass produces more forage in the once a week and every two weeks watering treatments, except in the CRP grazed plots. The result could merely be noise because of a higher order interaction of the three-way comparison. Forb forage production was found to be significant when I compared habitats (p=0.01). There was more forb production in the sagebrush plots (1.6 g, SE=0.4)] than the CRP plots (0.2 g, SE=0.2).

Forage production results for 2008 are presented in Table A.3.8. Perennial grass forage production differed by habitats (p=<0.01). The CRP plots produced 17.6 g (SE=2.9), while the sagebrush plots produced 3.1 g (SE=1.4). Forb forage production was greater in the sagebrush plots (1.1 g, SE=0.3) than the CRP plots (0.1 g, SE=0.1) when analyzed in terms of habitat (p=0.01).

Forage production results for 2009 are presented in Table A.3.9. Perennial grass forage production was greater in the CRP (17.6 g, SE=2.9) than sagebrush plots (3.1 g, SE=1.4) (p=<0.01). Forb production was greater in the sagebrush (1.1 g, SE=0.3) than CRP plots (0.1 g, SE=0.1) (p=0.01).

Arthropod Response

Arthropod results for 2007 are presented in Table A.3.10. Differences were found when comparing habitats, but not when comparing grazing and watering treatments. The orders Aranae (p=0.03), Diptera (p=<0.01), and Orthoptera (p=<0.01) were more abundant in CRP plots with means of 237.3 (SE=29.2), 502 (SE=53.0), and 331.4 (SE=32.0) individuals, respectively, than the sagebrush plots with means of 136.8 (SE=22.4), 211.3 (SE=34.8), and 100.3 (SE=17.9) individuals, respectively.

Arthropod results for 2008 are presetned in Table A.3.11. Again, differences were found when comparing between habitats, but not between grazing and watering treatments. Hemiptera (p=0.02) and Orthoptera (p=<0.01) were more abundant in CRP plots with means of 938.5 (SE=271.7) and 330.4 (SE=18.0) individuals, respectively, than in the sagebrush plots with means of 131.5 (SE=112.5) and 121.3 (SE=11.0) individuals. Homoptera (p=<0.01) and Lepidoptera (p=0.01) were more abundant in

sagebrush plots with means of 727.0 (SE=66.8) and 53.2 (SE=11.9) individuals, respectively, than in the CRP plots with means of 345.6 (SE=46.5) and 9.8 (SE=5.4) individuals, respectively. When analyzed by habitat and water treatment, Hemiptera differed (p=0.01), but when analyzed further this result did not follow the same pattern.

Arthropod results for 2009 are presented in Table A.3.12. Orthoptera were more abundant in the CRP plots with a mean of 341.7 (SE=23.9) individuals than the sagebrush plots with a mean of 105.7 (SE=13.5) individuals (p=<0.01).

Most of the individuals captured in the CRP plots belonged, in decreasing order, to Hymenoptera (ants, 22%), Hemiptera (21%), Homoptera (19%), Orthoptera (10%), Diptera (9%), Coleoptera (8%), Araneae (7%), Hymenoptera (bees and wasps, 5%), and Lepidoptera (0.3%). The majority of individuals captured in sagebrush plots belonged, in decreasing order, to Homoptera (34%), Hymenoptera (ants, 28%), Coleoptera (10%), Diptera (6%), Araneae (5%), Hemiptera (5%), Hymenoptera (bees and wasps, 5%), Orthoptera (4%), and Lepidoptera (1%). All orders occurred in both habitats.

Sage-grouse Use

Pellet count transects were conducted in May and July of 2007, 2008, and 2009. Pellets were only found during the counts in May 2007. These pellets were found on four adjacent plots in the sagebrush habitat. After examination it was determined that these pellets were left during the winter months and not during the nesting or brood-rearing period. Because of heavy snowfall that winter, I believe grouse used this area because it was located on a windswept ridge, leaving more sagebrush exposed (Ward 2006). In

conclusion, I found no evidence of grouse finding and using the brood-rearing areas created by my study.

DISCUSSION

A combination of factors contributed to and continues to exacerbate sage-grouse population declines. Declining populations have been characterized as exhibiting poor recruitment attributed to loss or fragmentation of brood-rearing habitats (Connelly et al. 2004). Concomitantly, the creation or restoration of mesic brood-rearing habitats in xeric environments has been identified as a conservation priority by regional and local sage-grouse working groups. These areas typically provide a higher abundance and diversity of forbs and arthropods essential to the diets of young chicks (Peterson 1970, Wallestad 1971, Klott and Lindzey 1990, Johnson and Boyce 1990, Sveum et al. 1998, Connelly et al. 2000, Crawford et al. 2004). The availability of forbs and arthropods has been positively associated with survival and recruitment of sage-grouse chicks.

The two most important habitats for Gunnison sage-grouse in San Juan County, Utah are CRP fields and areas of native sagebrush (Lupis 2005, Ward 2006). Over time wet meadow areas in each of these habitats have been reduced through changes in land use, therefore decreasing the habitat available to grouse during the brood-rearing season.

My study evaluated the role of irrigation and dormant season cattle grazing as practical management tools to create brood-rearing habitat in CRP and sagebrush. Although irrigated study plots retained their greenness longer in the growing season, I did not record any differences in vegetation or arthropod abundance and diversity because of irrigation or grazing. I did, however, note differences in vegetation and arthropod

composition between habitat types. The CRP plots studied contained greater arthropod diversity and abundance than native sagebrush plots. However, CRP plots were not equivalent to the native sagebrush plots in terms of providing vegetation essential for brood-rearing.

Arthropod abundance and diversity was higher in the CRP plots than in the sagebrush plots possibly because of the different vegetation communities the two habitats supported. The highest overall arthropod diversity values were obtained from the non-native CRP grassland habitat even though it had less vegetation diversity than the native sagebrush. This difference was not anticipated but could have occurred because the perennial grass (crested wheatgrass) of the CRP plots better suited the diets and feeding methods of the arthropods. CRP fields have been shown to support a high invertebrate biomass, even after losing their forb component, and have been proven to be an important habitat for songbirds and game birds that feed on arthropods (Hull et al. 1996, McIntyre and Thompson 2003, Doxon and Carroll 2007).

Sagebrush contains secondary metabolites as an antiherbivore defense that may act as toxins or digestion inhibitors with increasing concentration during the growing season of spring and summer (Wallestad and Eng 1975, Shipley et al. 2006, Wiens et al. 1991). Wiens et al. (1991) examined the secondary metabolites of sagebrush leaf tissue, and its effects on the abundance and diversity of arthropods. The study found that after an herbivorous attack by arthropods, sagebrush increased their level of toxins and the number of arthropods on the shrubs decreased. Sap and phloem feeding insects recovered more quickly than chewing insects. The feeding methods of sap and phloem

feeders may permit them to be highly discriminatory and avoid plant tissues containing secondary metabolites. Herbivorous leaf chewers were less likely to be able to discriminate among cell and tissue types within leaves and will therefore encounter more chemical compounds.

The differences I observed in the vegetation between the two habitats were expected. Land enrolled in CRP was once plowed agricultural land. This practice eliminated most of the sagebrush from the system and probably most of the seed bank supporting native forbs and grasses, and potentially changed the nutrient content of the soil. The seed mixture used in CRP fields was designed to establish a perennial grass cover, therefore it was expected that the CRP plots would have a greater occurrence of perennial grasses and little sagebrush. It was also expected that what sagebrush had begun to re-establish in the CRP plots would be smaller than those in the native sagebrush plots that had never been cultivated.

After the original seeding of the CRP fields, little if no sagebrush successfully established from seed (G. Wallace, Utah Division of Wildlife Resources, personal communication). Forbs successfully established from the seed mixture and remained in the system for a few years and then began to disappear. For this reason, few of those forbs still remained in the plots. Forbs that did occur in the CRP plots were invasive weeds, such as Russian knapweed (*Centaurea repens*), African mustard (*Malcomia africana*), and Russian thistle (*Salsola pestifer*). Crested wheatgrass was the one plant from the original mixture that remained in the system and was found to dominate the CRP plots.

Crested wheatgrass has been shown to develop monoculture stands and dominate plant communities for decades following establishment (Hull and Klomp 1967, Dormaar et al. 1995). The species has been shown to thicken and spread into adjacent areas (Hull and Klomp 1967). Its rapid dispersal rate and long-term dominance over and exclusion of native species have resulted in it being called an invader (Schuman et al. 1982, Henderson and Naeth 2005). Dormaar et al. (1995) found that altering the plant community from native mixed prairie to sequences of cropping followed by introduced grass monocultures significantly reduced the chemical quality of the soils by decreasing the root mass and organic matter evident in the top 7.5 cm of the soil, therefore reducing the energy flow into the soil system. Crested wheatgrass has been to shown to have less live root biomass and a high accumulation of aboveground dead material (Redente et al. 1989). The species allocated nearly twice the amount of carbon to aboveground photosynthetic tissue than plants in the blue grama ecosystem.

Stands of crested wheatgrass also tend to be very stable (Marlette and Anderson 1986). Stand stability was found to be largely a consequence of its dominance in the seed bank (Marlette and Anderson 1986, Henderson and Naeth 2005). Seed banks in crested wheatgrass stands support little diversity. There is little evidence that propagules from native communities are widely dispersed into adjacent crested wheatgrass stands and accumulate to form a diverse seed bank.

The results of this study support previous studies conducted on crested wheatgrass. It appeared that the native seed bank within the CRP plots had been lost. This probably occurred during the decades the land was under cultivation, time

dominated by crested wheatgrass, and lack of native seed dispersal from nearby areas (Marlette and Anderson 1986). The seeds from the original seed mixture seem to have also been lost. This could have occurred because of competition from crested wheatgrass, the effect of the species on the soil, and its dominance of the seed bank (Hull and Klomp 1967, Marlette and Anderson 1986, Redente et al. 1989, Dormaar et al. 1995, Henderson and Naeth 2005).

Seeding crested wheatgrass may inhibit or even preclude the development of a diverse plant community by retarding the recovery of native vegetation (Hull and Klomp 1967, Marlette and Anderson 1986). Monoculture stands have resisted the reintroduction of native species and maintained low species diversity (Marlette and Anderson 1986, Dormaar et al. 1995). A monoculture cannot be restored to a diverse plant community simply by removing some crested wheatgrass plants. If an increase in species diversity is desired, existing crested wheatgrass and their propagules in the soil must be destroyed and other species deliberately introduced. To improve the chances of creating brood-rearing habitat in CRP fields it might be necessary to physically remove or reduce the number of crested wheatgrass plants in the treatment areas and re-seed the plots with a mixture of native annual and perennial grasses and forbs. It may also be necessary to invest in proper seed bank preparation techniques and irrigation to ensure seed germination, seedling survival, and species persistence.

Irrigation of plots within each habitat resulted in the lengthening of the growing season for vegetation, but did not result in the anticipated increase in abundance and diversity of forbs, grasses, and arthropods. Vegetation in watered plots remained green

throughout the entire watering season (June to July) while vegetation in the control plots desiccated by the end of July. If a consistent watering pattern is continued over large areas and long periods of time, it might be possible for an abundant and diverse arthropod community to develop.

I found that using a sprinkler irrigation system was not efficient enough to produce the desired results. Using sprinklers was time consuming and required considerable maintenance. In the undulating landscape of the study area it was difficult to maintain water pressure in the pipes. The sprinklers were inefficient in the windy environment and because of strong daily afternoon winds I was forced to split the watering schedule in two, with a morning watering period and an evening watering period. In order for an irrigation method to be developed into a land management practice for creating brood-rearing habitat a different water delivery system will be necessary.

Although, this study did not provide the anticipated results, it did reveal important information about the vegetation and arthropod communities in both CRP and sagebrush that will affect the development of future management techniques, especially when managing CRP. During the study, I recorded an increase in vegetation growth and diversity in areas where leaks occurred in the irrigation system and water kept the soil saturated throughout the summer. This has led me to the conclusion that it is necessary to keep the soil saturated throughout the summer through flood irrigation. Solar panel powered pumps can be used to easily distribute water to certain areas. The use of the solar panel will allow the pump to run under its own power throughout the day while the

sun is shining. Distributing the water to low lying areas through a network of pipes will allow a large area of soil to be saturated throughout the summer. This method would reduce maintenance costs and the amount of labor required, while promoting perennial grass, forb, and sagebrush growth.

Future management techniques will also need to control crested wheatgrass. During this study, even under heavy dormant season cattle grazing, crested wheatgrass continued to dominate the CRP plots at the expense of forbs. Techniques should also address possible invasion by cheatgrass and other invasive weeds, while promoting the growth of native perennial grasses, forbs, and sagebrush. Possible techniques to accomplish this are a combination of mechanical disking, grazing, re-seeding of native perennial grasses and forbs, planting of sagebrush seedlings, and irrigation. This information can be used by managers and private landowners to implement brood-rearing restoration projects.

MANAGEMENT IMPLICATIONS

The creation of brood-rearing habitat is crucial for the recruitment of individuals into grouse populations. Techniques employed in these restoration projects could be developed into a cost-share program under EQIP. Restoration projects in CRP will require biological and mechanical treatments. The use of irrigation for the creation of brood-rearing habitat is essential to ensure the establishment and continued propagation of seeded perennial grasses and forbs, and sagebrush seedlings. Irrigation on public and private land is both a feasible and practical method when using solar powered groundwater pumps and flood irrigation. Control of crested wheatgrass will also be

necessary. Cattle grazing and mechanical disking are methods that could be used to control crested wheatgrass. These methods should be used in combination with re-seeding and flood irrigation.

LITERATURE CITED

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas, eds. 2001. Introduction to distance sampling—Estimating abundance of biological populations: Oxford University Press, Oxford, United Kingdom.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Dahlgren, D. 2005. Greater sage-grouse brood-rearing habitat manipulation in mountain big sagebrush, use of treatments, and reproductive ecology on Parker Mountain, Utah. Thesis, Utah State University, Logan, USA.

Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33:43-64.

Dormaar, J.F., M.A. Naeth, W.D. Willms, and D.S. Chanasyk. 1995. Effect of native prairie, crested wheatgrass (*Agropyron cristatum* (L.) Gareth.) and Russian wildrye (*Elymus junceus* Fish.) on soil chemical properties. Journal of Range Management 48:258-263.

Doxon, E.D., and J.P. Carroll. 2007. Vegetative and invertebrate community characteristics of Conservation Reserve Program fields relative to gamebirds in western Kansas. The American Midland Naturalist 158:243-259.

Drut, M.S., W.H. Pyle, and J.A. Crawford. 1994. Diets and food selection of sage-grouse chicks in Oregon. Journal of Range Management 47:90-93.

Graham, T.B., A.M.D. Brasher, and R.N. Close. 2008. Mormon cricket control in Utah's west desert; evaluation of impacts of the pesticide diflubenzuron on nontarget arthropod communities: U.S. Geological Survey Open-File Report 2008–1305, 82 p. [http://pubs.usgs.gov/of/2008/1305/].

Gunnison Sage-grouse Rangewide Steering Committee (GSRSC). 2005. Gunnison Sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, USA.

Gunnison Sage-grouse Rangewide Steering Committee (GSRSC). 2007. Minimum Structural Vegetation Collection Guidelines for the Gunnison Sage-grouse. Colorado Division of Wildlife, Denver, USA.

Henderson, D.C., and M.A. Naeth. 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions 7:639-650.

Hull, A.C., and G.J. Klomp. 1967. Thickening and spread of crested wheatgrass stands on southern Idaho ranges. Journal of Range Management 20:222-227.

Hull, S.D., R.J. Robel, and K.E. Kemp. 1996. Summer avian abundance, invertebrate biomass, and forbs in Kansas CRP. Prairie Naturalist 28:1-12.

Johnson, G.D., and M.S. Boyce. 1990. Feeding trials with insect in the diet of sage-

grouse chicks. Journal of Wildlife Management 54:88-91.

Klebenow, D.A., and G.M. Gray. 1968. Food habits of juvenile sage-grouse. Journal of Range Management 12:80-83.

Klott, J.H., and F.G. Lindzey. 1990. Brood habitat of sympatric sage grouse and Columbian Sharp-tailed grouse in Wyoming. Journal of Wildlife Management 54:84-88.

Lukacs, P.M. 2001. Estimating density of animal populations using trapping webs—Evaluation of web design and data analysis. Colorado State University, Fort Collins.

Lukacs, P.M. 2002. WebSim—Simulation software to assist in trapping web design. Wildlife Society Bulletin, v. 30, p. 1259−1261.

Lukacs, P.M., A.B. Franklin, and D.R. Anderson. 2004. Passive approaches to detection in distance sampling, Pages 260-280 *in* Buckland and others, editors. Advanced distance sampling—Estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

Lupis, S.G. 2005. Summer ecology of Gunnison Sage-grouse (*Centrocercus minimus*) in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Lupis, S.G., T.A. Messmer, and T. Black. 2006. Gunnison sage-grouse use of Conservation Reserve Program fields in Utah and response to emergency grazing: a preliminary evaluation. Wildlife Society Bulletin 34:957-962.

Marlette, G.M., and J.E. Anderson. 1986. Seed bank and propagule dispersal in crested wheatgrass stands. Journal of Applied Ecology 23:161-175.

McIntyre, N.E., and T.R. Thompson. 2003. A comparison of Conservation Reserve Program habitat plantings with respect to arthropod prey for grassland birds. The American Midland Naturalist 150:291-301.

New, T.R. 1998. Invertebrate surveys for conservation. Oxford University Press, Oxford, United Kingdom.

Olsen, M.E., L. Wilson, J.W. Metcalf, and T.B. Hutchings. 1962. Soil survey of the San Juan Area, Utah. Series 1945, No. 3. Utah Agricultural Experiment Station.

Peterson, J.G. 1970. The food habits and summer distribution of juvenile sage-grouse in central Montana. Journal of Wildlife Management 34:147-155.

Redente, E.F., M.E. Biondini, and J.C. Moore. 1989. Observations on biomass dynamics of a crested wheatgrass and native short grass ecosystem in southern Wyoming. Journal of Range Management 42:113-118.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2000. Gunnison Sage-grouse Conservation Plan, San Juan County, Utah.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2003. Gunnison Sage-grouse Conservation Plan Update San Juan County, Utah.

Schuman, G.E., F. Rauzi, and D.T. Booth. 1982. Production o Russian wildrye and crested wheatgrass and their effect on prairie soils. Agronomy Journal 74:23-26.

Shipley, L.A., T.B. Davila, N.J. Thines, and B.A. Elias. 2006. Nutritional requirements and diet choices of the pygmy rabbit (*Brachylagus idahoensis*): A sagebrush specialist. Journal of Chemical Ecology 32:2455-2474.

Sveum, C.M., J.A. Crawford, and W.D. Edge. 1998. Use and selection of brood-rearing

habitats by sage-grouse in south central Washington. Great Basin Naturalist 58:344-351.

Triplehorn, C.A., and N.F. Johnson. 2005. Borror and DeLong's introduction to the study of insects. Seventh edition. Thomson Brooks/Cole, Belmont, Calif.

USDI-BLM, Interagency Technical Team. 1996. Utilization Studies and Residual Measurements. Technical Reference 4400-3, BLM/RS/ST-96/004+1730, USDI-BLM, National Applied Resource Sciences Center.

Wallestad, R.O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129-136.

Wallestad, R.O., and R.L. Eng. 1975. Foods of adult sage-grouse in central Montana. The Journal of Wildlife Management 39:628-630.

Ward, S. 2006. Gunnison Sage-grouse winter ecology and arthropod abundance diversity in relation to habitat use in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Wiens, J.A., R.G. Cates, J.T. Rotenberry, N. Cobb, B. Van Horne, and R.A. Redak. 1991. Arthropod dynamics on sagebrush (*Artemisia tridentata*): effects of plant chemistry and avian predation. Ecological Monographs 61:299-321.

CHAPTER 3

ASSESSMENT OF VEGETATION CONDITIONS OF SAGEBRUSH HABITATS WITHIN THE GUNNISON SAGE-GROUSE CONSERVATION AREA IN SAN JUAN COUNTY, UTAH

ABSTRACT San Juan County supports the only population of Gunnison sage-grouse (*Centrocercus minimus*) found in Utah. The current population estimates are below the minimum desired population objective established in the Gunnison Sage-grouse Rangewide Conservation Plan (RCP) and the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP). Both plans identified the need to complete periodic assessments of the existing vegetation conditions in occupied and potential (unoccupied) sage-grouse habitat to ensure compliance with recommended guidelines and guide management actions. In the summer of 2009 I completed a habitat assessment of the 1,392,812 ha Gunnison Sage-grouse Conservation Area (CA) in San Juan County using RCP protocols. Using randomly generated points I measured vegetation conditions at 93 sites within occupied and unoccupied sagebrush habitats within the CA. Occupied habitat was defined as use areas contained within the 24,177 ha Conservation Study Area (CSA). Unoccupied habitat was defined as historical areas that previously supported sage-grouse or were in close proximity to areas that were currently or historically inhabited. I compared the current vegetation conditions for breeding, summer/fall, and winter habitats to RCP recommended guidelines. Perennial grass cover and height met or exceeded guidelines for occupied and unoccupied areas for all habitat categories. This was attributed largely to the introduction of crested wheatgrass (*Agropyron cristatum*)

into the system via the Conservation Reserve Program. Forb cover in unoccupied areas for all habitats approximated guidelines. In occupied areas forb cover was below RCP recommendations for all habitats. Forb cover height met the lowest limits of the guidelines for occupied and unoccupied areas for summer/fall but not breeding habitats. Sagebrush cover met or exceeded recommended guidelines for occupied and unoccupied areas for breeding and summer/fall habitats, but not winter habitats. Sagebrush (*Artemisia tridentata*) height met or exceeded guidelines for unoccupied and occupied areas for all habitat categories. To maximize habitat benefits for Gunnison sage-grouse in San Juan County, managers should implement conservation actions that protect existing sagebrush habitats and increase forb and grass cover in currently occupied habitats. This information will assist the Monticello/Dove Creek Local Working Group in prioritizing conservation efforts.

INTRODUCTION

Connelly et al. (2004) suggested that of the factors contributing to range wide declines in sage-grouse (*Centrocercus* spp.), the loss, degradation, and fragmentation of the sagebrush (*Artemisia* spp.) ecosystem were paramount. As sagebrush obligates, sage-grouse require sagebrush habitats to complete their life cycle. Thus, structure and composition of plant communities within sagebrush ecosystems influence sage-grouse nesting, breeding, brood-rearing, fall, and winter habitat selection.

Gunnison sage-grouse (*C. minimus*) currently occupy 4,787 km^2 (8.5% of their original range) in Colorado and Utah. There is one known population in the state of Utah. The Gunnison Sage-grouse Rangewide Conservation Plan (RCP) and the San Juan

County Gunnison Sage-grouse Conservation Plan (SJCCP) recommended management strategies to conserve the species (SWOG 2000, GSRSC 2005). Both plans identified the need for periodic habitat assessments to determine if existing vegetation conditions meet the desired vegetation criteria stated in the RCP. Periodic habitat assessments can assist managers in developing and prioritizing habitat restoration projects (GSRSC 2005).

The RCP established vegetation condition goals for Gunnison sage-grouse seasonal habitats (GSRSC 2005). Breeding habitats include lek, nesting, and early brood-rearing habitat from mid-March through late-June. The RCP defined breeding habitat as sagebrush communities delineated within 6.4 km of a lek. The SJCCP identified a long-term goal of reestablishing desired vegetation conditions on 50-75% of the area within 6.4 km of occupied lek sites (SWOG 2003). The defined vegetation characteristics for breeding habitats included: total shrub canopy cover of 20-40% (15-25% sagebrush canopy cover) with an average sagebrush height of 25-50 cm, 10-30% grass canopy cover with a height of 10-15 cm, and 5-15% forb canopy cover with a height of 5-10 cm (GSRSC 2005).

The RCP defined summer/fall habitat as vegetation communities, including sagebrush, agricultural fields, and wet meadows that are within 6.4 km of lek sites (GSRSC 2005). The SJCCP recommended establishing these conditions on 50-75% of the area (SWOG 2003). The defined desired vegetation conditions identified were: 10-30% total shrub canopy cover (5-15% sagebrush canopy cover) with an average sagebrush height of 20-40 cm, 10-25% grass canopy cover with a height of 10-15 cm, and 5-15% forb canopy cover with a height of 3-10 cm (GSRSC 2005). Mesic areas

should support a grass cover of 10-35% with a height of 10-15 cm and a forb cover of 15-35% with a height of 5-10 cm.

The SJCCP further identified the need to reestablish desired vegetation conditions of wintering habitats on 50% of the areas located within the Conservation Study Area (CSA) and 25% within the area buffering the CSA (SWOG 2003). Lupis (2005) and Ward (2007) previously defined the CSA based on location data obtained from radio-collared sage-grouse. The RCP defined winter habitat as sagebrush areas within currently occupied habitats that are available to sage-grouse in average winters (GSRSC 2005). The defined vegetation conditions for winter habitat include: sagebrush canopy cover of 30-40% with a height of 40-55 cm.

I completed a vegetation conditions assessment to determine the habitat conditions for Gunnison sage-grouse that inhabit San Juan County. This information will assist managers in quantifying the relative contribution of occupied and potential habitats to achieving overall SJCCP and RCP habitat and population goals. The results will be used by members of the Monticello/Dove Creek Local Working Group to update the current SJCCP, the RCP, and prioritize future conservation efforts.

STUDY AREA

The habitat assessment was conducted in San Juan County, Utah, during the summer of 2009. San Juan County is located in the extreme southeastern corner of Utah. The county is bordered by the Colorado River to the north and west, Arizona to the south, and Colorado to the east. The San Juan County Gunnison Sage-grouse Working Group (SWOG) previously designated an area northeast of the town of Monticello, Utah, as a

Gunnison sage-grouse priority conservation area (CA, Fig. 3.1, SWOG 2000). The CA consisted of 1,392,812 ha, 38% (127,170 ha) of which was privately owned. The CA was identified by encompassing historic and current lek sites, potentially suitable sage-grouse habitat, and sage-grouse observations. The CA was characterized by agricultural fields enrolled in the Conservation Reserve Program (CRP), active agricultural fields, and grazed interspersed with fragmented patches of Wyoming big sagebrush (*A. tridentata wyomingensis*), black sagebrush (*A. nova*), pinyon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), and oak (*Quercus gameblii*).

Within the CA, SWOG also identified the Conservation Core Area (CCA) that consisted of 136,249 ha, of which 89% (88,420 ha) was privately owned. Within the CCA, SWOG designated a priority study area, the CSA. The CSA consisted of 24,177 ha, of which 93% (22,556 ha) was privately owned. The CSA encompassed the current year round range of the population (Lupis 2005).

METHODS

In the summer of 2009, I measured vegetation parameters within Gunnison sage-grouse occupied and unoccupied habitats in San Juan County, Utah. I defined occupied habitat as areas located within the CSA. I defined unoccupied habitat as areas that were

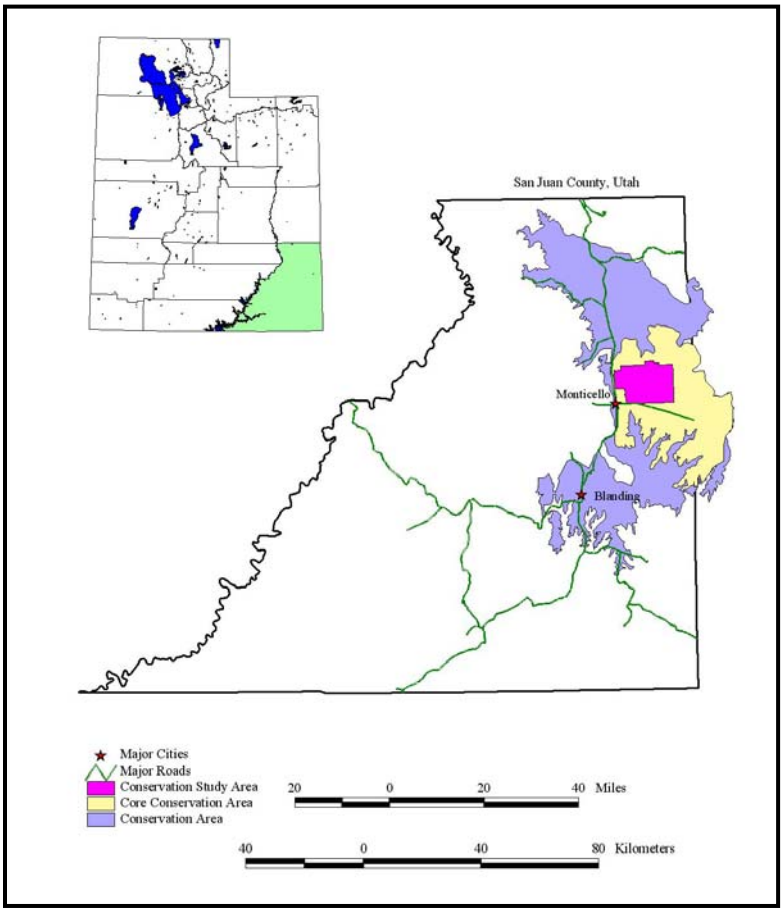


Figure 3.1. Gunnison Sage-grouse Conservation Area, San Juan County, Utah (Lupis 2005).

historically inhabited or were near an area currently or historically inhabited by sage-grouse. Unoccupied habitat largely fell within the CA and CCA. I compared these data to the habitat guidelines identified in the RCP to assess the status of existing and potential habitat in the CA, CCA, and CSA.

I conducted the habitat assessment by ground truthing LandSat imagery of the CA. I used ArcGIS (ArcMap version 9.3.1) to plot historic and current lek locations, which were located within the CSA. I created a polygon by buffering around the leks in

1,500 m increments to incorporate the distances the birds move from the leks throughout the year, such as from the lek to nesting areas, nesting areas to brood-rearing areas, and wintering areas (SWOG 2000, GSRSC 2005, Lupis 2005, Ward 2007). I further extended the buffer to include unoccupied habitat within the CCA and CA. After incorporating all possible movement distances and habitats the buffer totaled 7,500 m from lek sites (Fig. 3.2). Occupied habitats were confined to the CSA. Unoccupied habitats encompassed all other areas in the CA, excluding the CSA.

I generated 1,000 random points within the polygon and randomly selected 150 of these points (Fig. 3.2). Using satellite imagery I eliminated points that were located in agricultural fields, CRP, grazed rangelands, and pinyon-juniper and oak woodlands, focusing on points that encompassed sagebrush habitats, leaving 144 points. I visited each mapped point. Upon field visits some points were eliminated because they did not meet the established criteria. Points that fell within CRP, agricultural fields, woodlands, and grazed rangelands that did not support sagebrush were eliminated. Points that fell within private land posted as no trespassing were also eliminated. This left 93 points, 39 points in unoccupied and 54 points in occupied habitats, respectively.

At points that met the criteria, I measured the vegetation conditions using the Gunnison Sage-grouse Rangewide Steering Committee (GSRSC) Structural Vegetation Collection Guidelines (SVCG, GSRSC 2007). At each point, two 30-m transects were established. Cover of grasses, forbs, and shrubs was visually estimated by placing a Daubenmire frame every 3-m along each 30-m transect (Daubenmire 1959). The SVCG identified six cover classes based on the standardized Daubenmire method. The GSRSC

believed the Daubenmire method lumped too much vegetation into the 5-25% class for the Gunnison sage-grouse vegetation variables. Thus, they split the 5-25% category into 2 cover classes. The canopy cover classes used in this study were: 0-5%, 5-15%, 15-25%, 25-50%, 50-75%, 75-100% (GSRSC 2007).

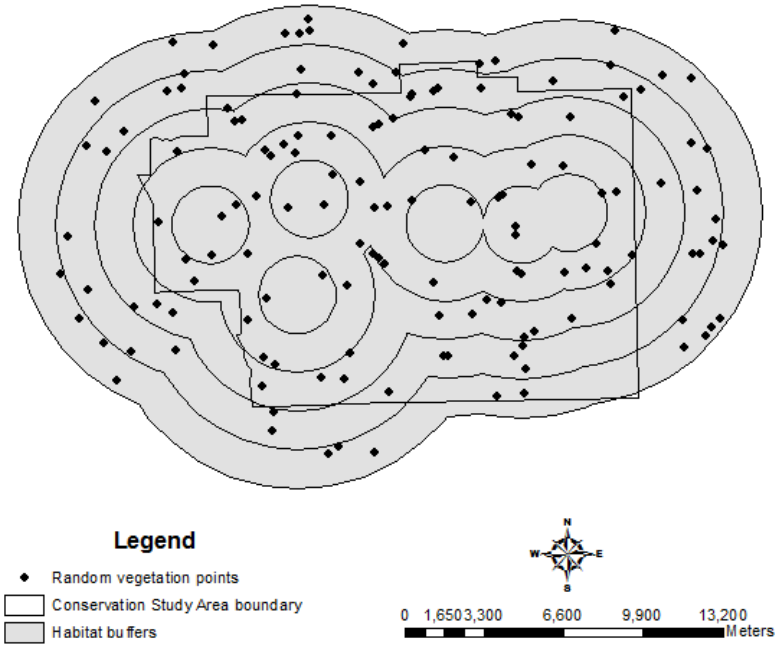


Figure 3.2. Buffer distances from active and historic leks to show seasonal movements of Gunnison sage-grouse (*Centrocercus minimus*) in and around the Conservation Study Area, San Juan County, Utah, 2009. Locations of randomly generated points used to assess habitat conditions in currently, historically, and potential habitat occupied by Gunnison sage-grouse. Occupied habitat is within the boundary of the Conservation Study Area. Unoccupied habitat is located outside of the Conservation Study Area boundary.

One height measurement of sagebrush, forb, annual grass, and perennial grass was taken at each Daubenmire frame by selecting the plant closest to the lower left hand corner of the frame (Daubenmire 1959, GSRSC 2007). If sagebrush was not found within the frame then the closest sagebrush within 10m of the frame was used. If no sagebrush was within 10m of the frame it was marked as not present. Only forbs and grasses within the frame were used to measure height. If no forb or grass was within the frame the plant group was marked as not being present.

DATA ANALYSIS

Vegetation data collected at each point were summed and averaged for each habitat area (occupied and unoccupied). Means for cover and height for each habitat area are reported with 95% confidence intervals. The results were then compared to the defined vegetation conditions recommended in the RCP for breeding, summer/fall, and winter habitat categories.

RESULTS

The RCP defines breeding and summer/fall habitat as the land within 6.4 km of lek sites (GSRSC 2005). This distance encompassed the entire CSA. As a result, all vegetation data collected at points within the CSA (n= 54) fell into the composite category encompassing breeding, summer/fall, and winter habitat.

Because sagebrush was the dominate shrub cover, I report total sagebrush cover in lieu of total shrub cover. The results for occupied and unoccupied habitat relative to RCP guidelines are presented in Table 3.1.

Occupied Habitat

In breeding habitats, perennial grass ($\bar{x}$=17%, CI=3.19) and sagebrush ($\bar{x}$=17%, CI=3.61) cover were within the RCP guidelines of 10-30% and 15-25%, respectively (Table 3.1). Forb cover ($\bar{x}$=3%, CI=1.40) did not meet the guidelines of 5-15%. Height of perennial grass ($\bar{x}$=23 cm, CI=4.39) was slightly above the guidelines of 10-15 cm. The height of sagebrush ($\bar{x}$=51 cm, CI=4.21) was within the upper limit of the guidelines of 25-51 cm. Forb height ($\bar{x}$=3 cm, CI=0.92) was below the guidelines of 5-10 cm.

In summer/fall habitats, cover of perennial grass ($\bar{x}$=17%, CI=3.19) was within the RCP guidelines of 10-25%. Sagebrush cover ($\bar{x}$=17%, CI=3.61) was within the upper limits of the guidelines of 5-15% cover. Cover of forbs ($\bar{x}$=3%, CI=1.40) was below the guidelines of 5-15%. Perennial grass height ($\bar{x}$=23 cm, CI=4.39) exceeded the guidelines of 10-15 cm. Forb height ($\bar{x}$=3 cm, CI=0.92) was at the lower limits of the guidelines of 3-10 cm. Sagebrush height ($\bar{x}$=51 cm, CI=4.21) exceeded the upper limits of 20-40 cm.

In winter habitats, cover of sagebrush ($\bar{x}$=17%, CI=3.6) was below the RCP guidelines of 30-40%. Sagebrush height ($\bar{x}$=51 cm, CI=4.21) exceeded the upper limits of 20-40 cm.

Unoccupied Habitat

In unoccupied breeding habitat, cover of perennial grass ($\bar{x}$=18%, CI=3.77), forbs ($\bar{x}$=6%, CI=1.64) and sagebrush ($\bar{x}$=17%, CI=4.40) were within the RCP guidelines of 10-30%, 5-15%, and 15-25%, respectively. Perennial grass height ($\bar{x}$=15 cm, CI=2.34) was also within the guidelines of 10-15 cm. Height of forbs ($\bar{x}$=4 cm, CI=0.72) was

below the guidelines of 5-10 cm. Sagebrush height ($\bar{x}$=46 cm, CI=4.64) was within the guidelines of 25-50 cm.

In unoccupied summer/fall habitats, cover of perennial grass ($\bar{x}$=18%, CI=3.77) and forbs ($\bar{x}$=6%, CI=1.64) were within the RCP guidelines of 10-25% and 5-15%, respectively. Cover of sagebrush ($\bar{x}$=17%, CI=4.40) slightly exceeded the guidelines of 5-15%. Height of perennial grass ($\bar{x}$=15 cm, CI=2.34) and forbs ($\bar{x}$=4 cm, CI=0.72) were within the guidelines of 10-15 cm and 3-10 cm, respectively. Sagebrush height ($\bar{x}$=46 cm, CI=4.64) exceeded the guidelines of 20-40 cm.

In unoccupied winter habitats, cover of sagebrush ($\bar{x}$=17%, CI=4.40) was below the guidelines of 30-40%. Sagebrush height ($\bar{x}$=46 cm, CI=4.64) was within the guidelines of 40-55 cm.

DISCUSSION

Based on the results of my habitat assessment of the vegetation parameters within occupied Gunnison sage-grouse habitats in the CA, CCA and CSA, I recommend that managers focus their attention on protection of existing sagebrush canopy cover and the

Table 3.1. Average percent cover and height of vegetation in occupied and unoccupied habitat in the Gunnison Sage-grouse (*Centrocercus minimus*) Conservation Area in San Juan County, Utah, 2009, reported with 95% confidence intervals. Occupied habitat was defined as land within the Gunnison Sage-grouse Conservation Study Area. Unoccupied habitat was defined as areas that once supported sage-grouse or were in close proximity to areas that support or once-supported sage-grouse. Unoccupied habitat fell within the Conservation Area and Core Conservation Area. Current habitat conditions were compared to habitat guidelines stated in the Gunnison Sage-grouse Rangewide Conservation Plan (GSRSC 2005).

	Percent Cover						Height (cm)					
Habitat	Perennial Grass	CI	Forbs	CI	Sagebrush	CI	Perennial Grass	CI	Forbs	CI	Sagebrush	CI
Measurments												
Occupied	17	3.19	3	1.40	17	3.61	23	4.39	3	0.92	51	4.21
Unoccupied	18	3.77	6	1.64	17	4.40	15	2.34	4	0.72	46	4.64
Guidelines												
Breeding	10-30		5-15		15-25		10-15		5-10		25-50	
Summer/fall	10-25		5-15		5-15		10-15		3-10		20-40	
Winter					30-40						40-55	

restoration of the forb components in CRP and native sagebrush. These observations are in line with the conservation strategies currently outlined in both the SJCCP and RCP.

Although unoccupied habitat in the CA better approximated SJCCP and RCP habitat guidelines, this area is avoided by Gunnison sage-grouse. Gunnison sage-grouse evolved in a landscape free of vertical structures, such as trees, power poles, and fence posts (Connelly, 2000*a*). Because of this evolutionary trait, they will avoid certain areas and will not cross over vertical structures even if the habitat on the other side is of good quality. Much of the area surrounding the occupied habitat confined within the CSA was dominated by pinyon-juniper and oak woodlands, therefore the birds will not cross over the trees to utilize these areas.

While ground truthing the randomly generated points that fell within unoccupied habitats in the CA, I discovered mosaics of open areas among the pinyon-juniper and oak woodlands. In many of these areas sagebrush could be found in small isolated patches, surrounded by or located near woodlands. Upon searching these patches, I did not find any evidence (i.e., pellets) that the sites were used by sage-grouse (Connelly et al. 2000*a*). Furthermore, when I overlaid the random points with known bird locations from previous studies, the locations were concentrated in the CSA (Fig 3.3). The small patches of sagebrush within the woodlands in the CA and CSA were avoided. The CSA was preferred by Gunnison sage-grouse because it contains little vertical structure in terms of oak and pinyon-juniper (Connelly et al. 2000*a*, GSRSC 2005).

Sage-grouse evolved in habitats free of vertical structures, including trees (Connelly et al. 2000*a*). Raptors and corvids prey on sage-grouse adults, young, and

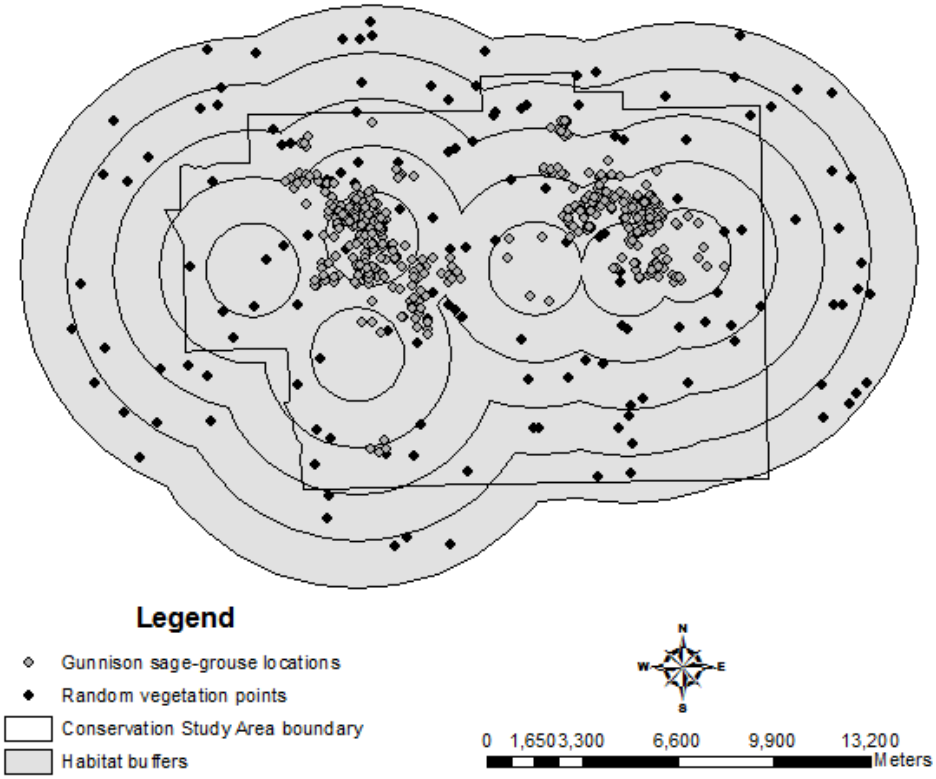


Figure 3.3. Location of vegetation monitoring points and known Gunnison sage-grouse locations within the Conservation Study Area, San Juan County, Utah, 2009 (Lupis 2005, Ward 2007).

nests. Previous research has shown that their presence increases with the presence of vertical structures (Hartzler 1974, Ellis 1984, Connelly et al. 2000*b*, Fletcher et al. 2003, Manzer and Hannon 2005). This not only increases possible predation of sage-grouse but also results in the fragmentation of habitat and populations by acting as a barrier and subdividing suitable habitat. The agricultural history of land use in the CSA may have contributed to the loss and fragmentation of sagebrush and corresponding reduction in

grass and forb cover. Currently, the dominant perennial grass throughout the CSA is crested wheatgrass (*Agropyron cristatum*). Crested wheatgrass was established in the CSA when thousands of hectares of cropland were originally enrolled in CRP and planted with a seed mixture that contained the non-native perennial grass (SWOG 2000). Crested wheatgrass has the potential to effectively out-compete native forbs and grasses and spread to adjacent areas (Hull and Klomp 1967, Schuman et al. 1982, Henderson andhas invaded sagebrush areas throughout the entire CSA, and it was more dominant than native perennial grasses at the sites evaluated.

Even though habitat quality in the CSA did not meet SJCCP and RCP habitat guidelines, the Gunnison sage-grouse population has steadily rebounded after an initial drop in the 1980s and has held steady over the past 20 years with only minor increases and decreases in response to drought conditions (Fig. 3.4, SWOG 2000, Lupis 2005).

I believe this rebound can be attributed largely to the advent of the CRP program in the CSA. Although CRP fields do not achieve vegetation habitat guidelines, these areas constitute new permanent contiguous vegetation cover that has provided Gunnison sage-grouse important seasonal habitats (Lupis 2005, Ward 2007). Thus, the retention and habitat restoration of CRP fields in the CSA for Gunnison sage-grouse should remain the highest conservation priority in San Juan County.

Reestablishing sagebrush, grass, and forb cover in CRP fields to approximate SJCCP and RCP guidelines would provide missing components to the habitat. These restoration efforts would help connect native sagebrush areas throughout the CSA, reducing the effects of fragmentation on the population.

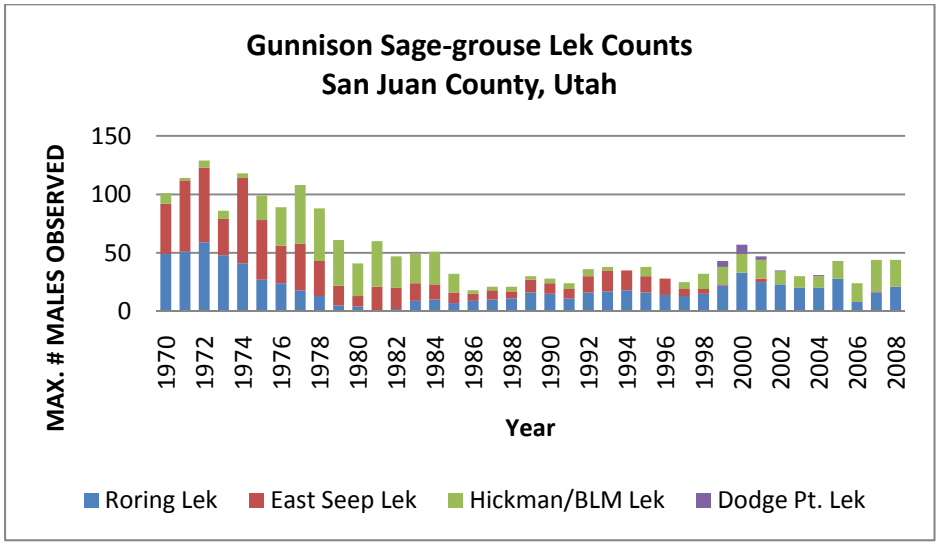


Figure 3.4. Gunnison Sage-grouse (*Centrocercus minimus*) lek counts from San Juan County, Utah. Maximum number of males observed is recorded. Data from Hickman and BLM leks have been combined because of daily movements of males between these 2 leks (SWOG 2004).

Later stages of habitat restoration efforts should focus on identifying areas outside of the CSA that hold promise for providing habitat for the sage-grouse. Restoration efforts designed to remove pinyon-juniper to open corridors would allow Gunnison sage-grouse access to areas exhibiting better habitats and facilitate population exchanges, which could increase genetic diversity. In the interim, managers should consider translocation of birds from both Colorado and Utah to mitigate concerns about low genetic diversity (GSRSC 2005).

MANAGEMENT IMPLICATIONS

The results of the habitat assessment illustrate that the sage-grouse are restricted to occupied habitats in the CSA by the presence of pinyon-juniper and oak woodlands. This exemplifies the need to improve the habitat within the CSA to maximize what little habitat the grouse have available to them. The habitat assessment also illustrated that forbs and grasses are lacking from much of the habitat within the CSA. Habitat improvement projects should be focused on the remaining sagebrush areas within the CSA. Efforts should also be made to re-establish sagebrush, forb, and grass patches within CRP fields throughout the CSA to expand the habitat available to the grouse.

LITERATURE CITED

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000*a*. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Connelly, J.W., A.D. Apa, R.B. Smith, and K.P. Reese. 2000*b*. Effects of predation and hunting on adult sage-grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6: 227-232.

Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation Assessment of Greater Sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming.

Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33:43-64.

Ellis, K.L. 1984. Behavior of leking greater sage-grouse in response to a perched golden

eagle. Western Birds 15: 37-38.

Fletcher, Q.E., C.W. Dockrill, D.J. Saher, and C.L. Aldridge. 2003. Northern harrier, *Circus cyaneus*, attacks on greater sage-grouse, *Centrocercus urophasianus*, in southern Alberta. Canadian Field Naturalist 117: 479-480.

Gunnison Sage-grouse Rangewide Steering Committee (GSRSC). 2005. Gunnison Sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, USA.

Gunnison Sage-grouse Rangewide Steering Committee (GSRSC). 2007. Minimum Structural Vegetation Collection Guidelines for the Gunnison Sage-grouse. Colorado Division of Wildlife, Denver, USA.

Hartzler, J.E. 1974. Predation and the daily timing of greater sage-grouse leks. Auk 91: 532-536.

Henderson, D.C., and M.A. Naeth. 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions 7:639-650.

Hull, A.C., and G.J. Klomp. 1967. Thickening and spread of crested wheatgrass stands on southern Idaho ranges. Journal of Range Management 20:222-227.

Lupis, S.G. 2005. Summer ecology of Gunnison Sage-grouse (*Centrocercus minimus*) in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Manzer, D.L., and S.J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: A multi-scale approach. Journal of Wildlife Management 69: 110-123.

Schuman, G.E., F. Rauzi, and D.T. Booth. 1982. Production of Russian wildrye and crested wheatgrass and their effect on prairie soils. Agronomy Journal 74:23-26.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2000. Gunnison Sage-grouse Conservation Plan, San Juan County, Utah.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2003. Gunnison Sage-grouse Conservation Plan Update San Juan County, Utah.

Ward, S. 2007. Gunnison sage-grouse winter ecology and arthropod abundance diversity in relation to habitat use in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

CHAPTER 4

RAPTOR AND CORVID RESPONSE TO POWER DISTRIBUITION LINE PERCH DETERRENTS IN UTAH

ABSTRACT Increased raptor and corvid abundance has been documented in landscapes fragmented by man-made structures, such as fence posts and power lines. These vertical structures may enhance raptor and corvid foraging and predation efficiency because of increased availability of perch, nesting, and roosting sites. Concomitantly, vertical structures, in particular power distribution lines, have been identified as a threat to sage-grouse (*Centrocercus* spp.) conservation. To mitigate potential impacts of power distribution lines on sage-grouse and other avian species, the electrical power industry has retrofitted support poles with perch deterrents to discourage raptor and corvid use. No published information is available regarding efficacy of contemporary perch deterrents on avian predator use of lower-voltage power distribution lines. We evaluated efficacy of 5 perch deterrents mounted on support poles of an 11-km section of a 12.5-kV distribution line that bisected occupied Gunnison sage-grouse (*C. minimus*) habitat in southeastern Utah, USA. Perch deterrents were mounted on the line in November–December 2006 following a random replicated block design that included controls. During 168 hours and 84 hours of direct observation in 2007 and 2008, respectively, we recorded 276 and 139 perching events of 7 potential avian predators of sage-grouse. Golden eagles (*Aquila chrysaetos*) were the dominant species we recorded during both years. We did not detect any difference in perching events by perch deterrent we evaluated and controls ($p > 0.05$). Perch deterrents we evaluated were not effective

because of inherent design and placement flaws. Additionally, previous pole modifications that mitigated avian electrocutions provided alternative perches. We did not record any raptor or corvid electrocutions or direct predation on Gunnison sage-grouse. The conclusions of this study can be applied by conservation groups and power companies to future management of power distribution lines within areas inhabited by species sensitive to man-made vertical structures.

INTRODUCTION

Transmission lines are defined as power lines designed and constructed to support voltages >60 kV (Avian Power Line Interaction Committee 2006). Distribution lines are defined as a circuit of low-voltage lines, energized at voltages from 2.4 kV to 60 kV and used to distribute electricity to residential, industrial, and commercial customers. The Western Association of Fish and Wildlife Agencies (J. W. Connelly, Western Association of Fish and Wildlife Agencies, unpublished report) reported ≥15,296 km^2 of current sage-grouse (*Centrocercus* spp.) range contained power transmission lines; however, the group was unable to map density of power distribution lines in rural areas.

Connelly et al. (2000b, Connelly, unpublished report) suggested that because of the potential for raptors and corvids to use transmission-line towers and distribution-line poles as new perches and nest sites, placement of these facilities in seasonal sage-grouse habitats could impact the species through increased predation of adults, juveniles, and nests or result in sage-grouse abandoning sites (Knight and Kawashima 1993, Knight et al.1995, Kochert and Olendorff 1999). Corvids and raptors prey on sage-grouse adults, young, and nests. Hartzler (1974), Ellis (1984), Connelly et al. (2000a), Fletcher et al.

(2003), and Manzer and Hannon (2005) reported the impact of avian predators on sage-grouse populations may be exacerbated in human-altered landscapes. Because of these concerns, the Gunnison Sage-Grouse Rangewide Steering Committee (2005) identified retrofitting of distribution line poles with perch deterrents to discourage raptors and corvids from perching as a priority species conservation strategy.

Previous studies have evaluated perch deterrents' effectiveness on transmission-line towers and towers associated with air traffic control (Michener 1928, Janss and Ferrer 1999, Kochert and Olendorff 1999, Avery and Genchin 2004). Lammers and Collopy (2007) studied effectiveness of perch deterrents on towers of a high-voltage (345 kV) transmission line that bisected habitats occupied by greater sage-grouse (*Centrocercus urophasianus*). However, no studies have been published that evaluate efficacy of perch deterrents on distribution lines. We studied raptor and corvid response to 5 types of perch deterrents mounted on a power distribution line that traversed occupied Gunnison sage-grouse habitat in southeastern Utah, USA. Our objective was to determine if raptor or corvid use of the distribution line differed by perch deterrent type or control.

STUDY AREA

We conducted our study during winters of 2007 and 2008 in the Gunnison sage-grouse Conservation Study Area (CSA) located in San Juan County, Utah, USA. The San Juan County Gunnison Sage-grouse Working Group (SWOG) previously identified the CSA. The CSA was located east of the town of Monticello, Utah, USA (SWOG 2005). The CSA contained the primary breeding and wintering complexes of the San

Juan County Gunnison sage-grouse population. The habitat within the CSA consisted of sagebrush (*Artemisia* spp.), grazed rangelands, agriculture fields, and croplands enrolled in the Conservation Reserve Program (CRP).

The study distribution line we selected for study was the longest continuous line located within the CSA. This line paralleled the northern edge of the CSA, which provided Gunnison sage-grouse winter habitat, and was located within 1 km of active leks (Lupis 2005, Ward 2007). The distribution line had a voltage rating of 12.5 kV and paralleled a well-maintained county road. The road allowed access during winter and across private land. The distribution line traversed an undulating landscape and a variety of habitats that included CRP fields, agriculture fields, grazed rangelands, and sagebrush.

METHODS

With the cooperation of PacifiCorp field crews, we established an experimental randomized block design for installation of perch deterrents, which controlled for differences in vegetation and landscape topography that could affect raptor and corvid pole preferences. This design eliminated sampling bias by ensuring that we evaluated each type of deterrent and control relative to habitat types and topography present throughout the length of the distribution line. We considered each pole an experimental unit. We divided the line into 14 blocks consisting of 6 poles each. Within a block, we randomly assigned each pole to one of the 5 treatments or control. The result was multiple replications of each treatment and the control across all habitat types and topographies present. Poles assigned as controls were not fitted with a deterrent.

In November–December 2006 an 11-km section of the selected distribution line, consisting of 84 poles, was modified by PacifiCorp field crews with 5 types of perch deterrents following manufacturer recommendations and in accordance with the established experimental design (Fig. 4.1a–f). Physical deterrents consisted of cones and triangles (Kaddas Enterprises Inc., Salt Lake City, UT), and mini-zenas (Prommel Enterprises Inc., Odenville, AL). The reflective hazing deterrent consisted of displaying single or paired FireFlies™ (P and R Technologies Inc., Portland, OR) suspended on the top and cross arm of the distribution pole. Because of differences in construction, some poles could not support the assigned deterrent, which resulted in incomplete blocks with 14 replications of control poles, mini-zenas, and the 1-FireFly and 2-FireFly arrangements; 16 replications of cones; and 12 replications of triangles.

We conducted perching surveys in 2007 and 2008. We initiated surveys in January and concluded them in April. We selected this survey period because it coincided with the peak number of wintering and migrating raptors and corvids in the area of the distribution line (G. Wallace, Utah Division of Wildlife Resources, personal communication). During this time period raptor and corvid numbers are increased by presence of migrant winter raptor species, including bald eagles (*Haliaeetus leucocephalus*) and rough-legged hawks (*Buteo lagopus*).



Fig. 4.1a.



Fig. 4.1b.

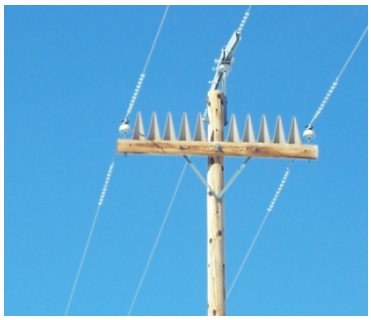


Fig. 4.1c.



Fig. 4.1d.



Fig. 4.1e.



Fig. 4.1f.

Figures 4.1 a-f. Five types of commercially available perch deterrents we evaluated included: a) single and b) paired arrangement of the FireFly™ (P and R Technologies Inc., Portland, OR) hazing deterrent; c) cones (Kaddas Enterprises Inc., Salt Lake City, UT); d) triangles (Kaddas Enterprises Inc., Salt Lake City, UT); e) spikes (Prommel Enterprises Inc., Odenville, AL); and f) control; San Juan County, Utah, 2007-2008.

We surveyed the distribution line twice a day, 5 days a week, weather permitting. We conducted surveys at 0800–1100 hr and 1400–1700 hr (Stahlecker 1978, Fuller and Mosher 1987). We randomly selected the starting point (west or east end) for each survey. We used alternative routes to arrive at the starting points to avoid disturbing any birds already perched. We spent 5 minutes at the starting point and at each mile point

thereafter observing and recording any birds seen. While driving to the mile points we maintained speed of the vehicle at 15–25 km/hour.

We recorded all birds perched on the distribution poles. We defined a perching event as an observation of a raptor or corvid perched on a pole. This number of perching events was not a reflection of the density of birds inhabiting the study area, as we could record one bird more than once if it continued down the line perching on different poles. Observations included species, numbers, and perch locations. We recorded exact positions of birds perched on individual poles within the study distribution line.

In our data analysis, we addressed the following questions: 1) did total count of perching events recorded by treatment and control in 2007 and 2008 differ by perch deterrent type and year, and 2) did total count for each species on each type of deterrent and control in 2007 and 2008 differ? The model we used compared means among treatments for total count of perching events and total species counts observed in 2007 and 2008. We used a generalized linear-mixed model with Poisson distribution and log link (SAS Institute, Cary, NC). We made pairwise comparisons among treatment means where necessary. Thus, the statistical model was 1-way in a randomized spatial block design, with poles grouped into spatial blocks to control for spatial heterogeneity in the landscape. We conducted data analyses using the GLIMMIX procedure in SAS–STAT for Windows Version 9.1.3 (SAS Institute).

RESULTS

During 168 hours and 84 hours of direct observation in 2007 and 2008, respectively, we recorded 253 and 136 perching events, respectively, of 7 potential avian predator species of sage-grouse (J. W. Connelly, Western Association of Fish and Wildlife Agencies, unpublished report). The most common perching events by species were golden eagles (*Aquila chrysaetos*), common ravens (*Corvus corax*), and rough-legged hawks. Other species included red-tailed hawks (*B. jamaicensis*), bald eagles, black-billed magpies (*Pica hudsonia*), and ferruginous hawks (*B. regalis*). For analysis we used golden eagle, common raven, and rough-legged hawk counts. Because of the small sample sizes for the other species they were excluded from our statistical analysis.

In 2007, we conducted 112 surveys and recorded 172 (68%) perching events on poles fitted with perch deterrents. Perching events recorded did not differ ($p > 0.05$) for controls (32%), triangles (25%), cones (22%), and minizenas (21%, p=0.31, Table 1). Number of perching events also did not differ by control and perch deterrent type for golden eagles (p=0.07), common ravens (p=0.67), or rough-legged hawks (p=0.71, Table 2). Golden eagles were the most common with 195 (77%) perching events, of which 128 (74%) were on poles fitted with perch deterrents.

In 2008, winter snow conditions periodically closed the survey road and reduced the number of surveys completed. We conducted 56 surveys and recorded 136 avian predator perching events with 91 (67%) events on poles fitted with perch deterrents. Perching events recorded did not differ (p>0.05) for controls (33%), cones (26%), mini-zenas (24%), or triangles (17%, p=0.15, Table 4.1). Number of perching events did not

differ by control and perch deterrent type for golden eagles (p=0.33), common ravens (p= 0.22), and rough-legged hawks (p=0.91, Table 4.2). Golden eagles were also most common in 2008 with 110 (81%) perching events, of which 76 (84%) were on poles fitted with perch deterrents. In both survey years, avian predators avoided deterrents, opting for alternative perch sites on the same pole such as insulators, bird guards, and deterrent-free parts of the cross arm, which allowed the birds to perch next to deterrents (Figs. 4.2a–f).

The structural design of the FireFly hazing deterrent could not withstand weather conditions. The FireFly was designed to spin in the wind, creating a reflective strobe effect intended to deter birds from perching. Average wind speed during the 2007 winter surveys was 19 km/hour, with gusts up to 74 km/hour. By the end of the 2007 survey period 10 of the 14 single Firefly arrangements and 11 of 14 double FireFly arrangements were damaged as a result of weather conditions and were largely inoperable, preventing us from evaluating their effectiveness as perch deterrents. Because part of the study design was to assess cost-effectiveness, including maintenance, we did not replace damaged FireFly arrangements prior to 2008 surveys. Thus, we did not analyze these data. Problems included 1) cracking at the site of the swiveling connector causing the reflector to break off of the unit, 2) support arms bending or breaking off under prevailing winds, and 3) swiveling connectors separating from their support base.

Table 4.1. Number of perching events (n) and percentage of perching events (%) by golden eagles, common ravens, and rough-legged hawks recorded documented on each perch deterrent tested and control power poles, and the estimated treatment mean ($\bar{x}$) with standard error (SE). San Juan County, Utah 2007 and 2008. The perch deterrents tested included: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL), and c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT).

	2007				2008			
Perch deterrent	n	%	$\bar{x}$	SE	n	%	$\bar{x}$	SE
Cones	56	22	3.9	0.87	36	26	2.0	0.47
Mini zena	54	21	3.9	0.83	32	24	2.1	0.47
Triangle	62	25	4.2	0.92	23	17	2.0	0.49
Control	81	32	5.1	1.05	45	33	3.2	0.62

DISCUSSION

Our study was the first to evaluate commercially available perch deterrents as a means to prevent perching on poles of distribution lines by avian predators that pose a threat to sage-grouse. Perch deterrents we evaluated were ineffective. Our results support those reported by Lammers and Callopy (2007) for 345-kV towers within a transmission line in occupied sage-grouse habitat. Lammers and Callopy (2007) reported that deterrents did not prevent perching but did reduce raptor perching duration. However, the transmission towers in their study were 23–40 m tall and spaced in 366-m intervals.

Table 4.2. Number of perching events (n) documented for golden eagles, common ravens, and rough-legged hawks by perch deterrent type and control, and *F*-statistics (*F*) and *P*-values (*P*), San Juan County, Utah 2007 and 2008. The perch deterrents tested included: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL), and c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT).

	2007						2008					
Species	Cones	Mini zena	Triangles	Control			Cones	Mini zena	Triangles	Control		
	n	n	n	n	*F*	*p*	n	n	n	n	*F*	*p*
Golden eagle	42	35	51	67	2.6	0.07	33	24	19	34	1.2	0.33
Common raven	9	13	8	7	0.5	0.46	1	6	3	8	1.5	0.22
Rough-legged hawk	5	6	3	7	0.5	0.71	2	2	1	3	0.2	0.91
Total	56	54	62	81	1.2	0.31	36	32	23	45	1.9	0.15



Fig. 4.2a.



Fig. 4.2b.

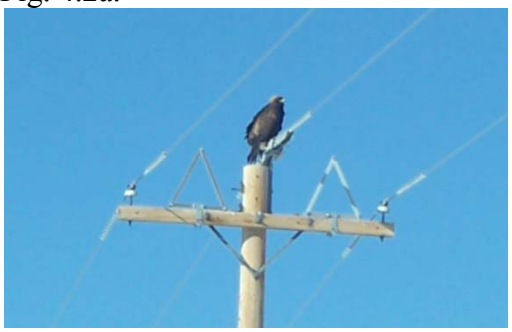


Fig. 4.2c.



Fig. 4.2d

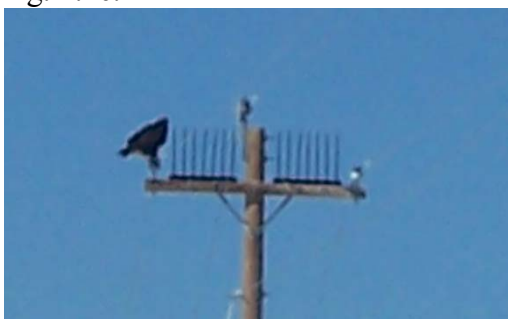


Fig. 4.2e.



Fig. 4.2f.

Figures 4.2a-f. Typical golden eagle perching events documented relative to perch deterrent type on power distribution poles: a) cones (Kaddas Enterprises Inc., Salt Lake City, UT), b) mini zenas (Prommel Enterprises Inc., Odenville, AL), c) triangles (Kaddas Enterprises Inc., Salt Lake City, UT), d) 2-FireFly™ (P and R Technologies Inc., Portland, OR) arrangement, e) mini zenas, and f) 1-FireFly™ arrangement, San Juan County, Utah, 2007 and 2008.

The deterrent they tested was designed for discomfort and placed on parts of towers where avian predators would most likely perch.

Effectiveness of perch deterrents we evaluated may have been affected by the structure of power poles and the basic design and placement of deterrents. Perch deterrents we tested were partially successful in that they had the ability to prevent perching on parts of the poles. However, birds continued to perch on parts of the poles without deterrents, such as insulators. A perch deterrent that covers insulators, in combination with physical deterrents we tested, has potential to prevent perching of avian predators on power poles of distribution lines.

Before any further evaluation of FireFly as a perch deterrent we recommend the current design be modified. Modifications should include increased durability of plastic reflectors, stronger support bases, and swivel connections that can better withstand weather extremes.

MANAGEMENT IMPLICATIONS

We found that current commercially available perch deterrents used to prevent avian species electrocutions did not mitigate potential avian predators of sage-grouse from perching on poles of a distribution line. For the perch deterrents we evaluated to be successful, they would need to be redesigned to retrofit all parts of the pole, including insulators, rather than just the cross arm. Deterrents must also be designed to better withstand weather extremes.

LITERATURE CITED

Avian Power Line Interaction Committee. 2006. Suggested practices for avian protection on power lines—the state of the art in 2006. Edison Electric Institute, Washington, D.C., USA.

Avery, M.L., and A.C. Genchi. 2004. Avian perching deterrents on ultrasonic sensors at airport wind-shear alert systems. Wildlife Society Bulletin 32:718–725.

Connelly, J.W., A.D. Apa, R.B. Smith, and K.P. Reese. 2000a. Effects of predation and hunting on adult sage-grouse (*Centrocercus urophasianus*) in Idaho. Wildlife Biology 6:227–232.

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000b. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Ellis, K.L. 1984. Behavior of lekking greater sage-grouse in response to a perched golden eagle. Western Birds 15:37–38.

Fletcher, Q.E., C.W. Dockrill, D.J. Saher, and C.L. Aldridge. 2003. Northern harrier, *Circus cyaneus*, attacks on greater sage-grouse, *Centrocercus urophasianus*, in southern Alberta. Canadian Field Naturalist 117:479–480.

Fuller, M.R., and J.A. Mosher. 1987. Raptor survey techniques. Pages 37–65 in B. G. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, editors. Raptor management techniques manual. National Wildlife Federation Scientific and Technical Series 10, Washington, D.C., USA.

Hartzler, J.E. 1974. Predation and the daily timing of greater sage-grouse leks. Auk

91:532–536.

Janss, G.F.E., and M. Ferrer. 1999. Mitigation of raptor electrocution on steel power poles. Wildlife Society Bulletin 27:263273.

Knight, R.L., and J.Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear rights-of-ways. Journal of Wildlife Management 57:266–271.

Knight, R.L., H.A.L. Knight, and R.J. Camp. 1995. Common ravens and number and types of linear rights-of-way. Biological Conservation 4:65–67.

Kochert, M.N., and R.R. Olendorff. 1999. Creating raptor benefits from power line problems. Journal of Raptor Research 33:39–42.

Lammers, W.M., and M.W. Collopy. 2007. Effectiveness of avian predator perch deterrents on electric transmission lines. Journal of Wildlife Management 71:2752–2758.

Lupis, S.G. 2005. Summer ecology of Gunnison sage-grouse (*Centrocercus minimus*) in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Manzer, D.L., and S.J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Michener, H. 1928. Where engineer and ornithologist meet: transmission line troubles caused by birds. Condor 30:169–175. San Juan County Gunnison Sage-Grouse Working Group [SWOG]. 2005. Gunnison sage-grouse annual report. San Juan County, Utah, USA.

Stahlecker, D.W. 1978. Effect of a new transmission line on wintering raptors. Condor

80:444–446.

Ward, S. 2007. Gunnison sage-grouse winter ecology and arthropod abundance and diversity in relation to habitat use in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

CHAPTER 5

CONCLUSIONS

Gunnison sage-grouse (*Centrocercus minimus*) currently occupy 8.5% of their presumed historical range (Schroeder et al. 2004). The decline has been attributed to the loss or conversion of sagebrush (*Artemisia* spp.) to other land uses. The quality of the remaining habitat has been impacted by urbanization, grazing, agriculture and fragmentation. As a result, the Gunnison sage-grouse is limited to seven known populations in Colorado and one population in southeastern Utah (GSRSC 2005). The only known Gunnison sage-grouse population in Utah occurs in San Juan County, Utah, near the town of Monticello.

The San Juan County Gunnison Sage-grouse Working Group (SWOG) previously designated an area northeast of the town of Monticello as a sage-grouse priority conservation area (SWOG 2000). The Conservation Area (CA) consisted of 1,392,812 ha, 38% (127,170 ha) of which is privately owned. The CA was identified by encompassing historic and current lek sites, potentially suitable sage-grouse habitat, and sage-grouse observations. The CA is characterized by large fields enrolled in the Conservation Reserve Program (CRP), agricultural fields, and grazed rangelands interspersed with fragmented patches of Wyoming big sagebrush (*A. tridentata wyomingensis*), black sagebrush (*A. nova*), pinyon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), and oak (*Quercus gambelii*). Within the CA, SWOG also identified a Core Conservation Area (CCA) that consisted of 136,249 ha, of which 89% (88,420 ha) was privately owned. Within the CCA, a Conservation Study Area (CSA) was also identified.

The CSA consisted of 24,177 ha, of which 93% (22,556 ha) was privately owned. The CSA encompassed currently occupied habitat (Lupis 2005, Ward 2007).

The Gunnison Sage-grouse Rangewide Conservation Plan (RCP) and the San Juan County Gunnison Sage-grouse Conservation Plan (SJCCP) recommend management strategies to address identified conservation threats to the San Juan County population (SWOG 2000, GSRSC 2005). Current management of Gunnison sage-grouse in San Juan County, Utah, was based on studies that gathered information regarding the population's life history, habitat use, and movement patterns (Lupis 2005, Ward 2007). This information was used by the Monticello/Dove Creek Local Working Group to guide conservation and management strategies stated within the SJCCP. The research I conducted addressed three conservation strategies identified in the SJCCP: 1) the creation and enhancement of brood-rearing areas; 2) the assessment of habitat conditions within the CA; and 3) the prevention or reduction of perching events by raptors and corvids on distribution line power poles.

The RCP and the SJCCP identified protection and enhancement of mesic brood-rearing habitats as a priority conservation strategy. Increased availability of forbs and arthropods in brood-rearing habitats has been positively associated with survival and recruitment of sage-grouse chicks (Peterson 1970, Wallestad 1971, Klott and Lindzey 1990, Johnson and Boyce 1990, Sveum et al. 1998, Connelly et al. 2000, Crawford et al. 2004). From 2007-2009, I evaluated the role of irrigation in creating mesic or wet meadow environments and dormant season grazing by cattle on habitat quality as measured by changes in vegetation structure and composition, arthropod abundance and

diversity, and sage-grouse use. I conducted the experiment on 24 randomly selected 0.1 ha plots located in agricultural lands enrolled in CRP and native sagebrush.

Observationally, the vegetation in the irrigated plots remained greener longer through the season than in the non-irrigated plots, but vegetation diversity did not differ ($p>0.01$). The CRP plots exhibited greater arthropod abundance and cover of perennial grass than the native sagebrush plots, but lower diversity of perennial grasses and abundance and diversity of forbs ($p<0.01$). Crested wheatgrass (*Agropyron cristatum*) was the dominant species in the CRP plots and may have out-competed native forbs and grasses (Hull and Klomp 1967, Schuman et al. 1982, Henderson and Naeth 2005). Dormant season grazing of the CRP plots did not reduce crested wheatgrass cover but did eventually remove residual growth from previous seasons. Lastly, I did not detect any increased sage-grouse use of the treatment plots. This observation may be an artifact of the small plot size and isolated locations.

The increased arthropod abundance in CRP plots relative to the native sagebrush plots and the increased greenness of vegetation because of irrigation suggests a role for irrigation in managing these areas as brood-rearing habitats. The sprinkler irrigation system used in this study allowed quantification of water application rates. However, because of frequent winds, this system did not provide uniform plot coverage and may have resulted in increased evaporation. Thus, creation of mesic areas in brood-rearing habitats may best be accomplished by a system of terraces, ditch plugs or small check dams that retain moisture longer, and by providing flood irrigation. To increase forb and grass diversity in CRP, managers should evaluate the use of mechanical treatments,

coupled with spring grazing and reseeding to mitigate the potential competitive effects of crested wheatgrass.

The second conservation strategy I addressed was the assessment of habitat conditions within the CA. In the summer of 2009 I used randomly generated points to measure vegetation conditions within habitat unoccupied and currently occupied by Gunnison sage-grouse. I compared the measured vegetation characteristics with the criteria for desired vegetation conditions outlined within the RCP. The results of the habitat assessment showed that sage-grouse movement and habitat use may be restricted to the CSA by the presence of pinyon-juniper and oak woodlands that surround the area. Because the woodlands occupy larger areas surrounding the CSA and do not provide sagebrush habitats, they may impede population exchanges between Utah and Colorado. These wooded areas are also avoided by the grouse because they provide perch sites for avian predators. These observations highlight the need to improve the habitat within the CSA to maximize the benefits of the habitat the grouse have available to them. Once habitat quality in the CSA approaches SJCCP and RCP guidelines, management actions should focus on opening corridors through these woodlands to facilitate population interchange. In the meantime, managers should consider species translocation between both Colorado and Utah to increase the genetic diversity in both populations.

The habitat assessment verified that forb and grass cover in the CSA is below SJCCP and RCP recommendations. Habitat improvement projects should be focused on retaining and enhancing the habitat quality of remaining sagebrush areas within the CSA. In particular, management efforts should be renewed to re-establish sagebrush, forb, and

grass cover within CRP fields throughout the CSA to expand the habitat available to the grouse.

Connelly et al. (2000, Connelly et al., Western Association of Fish and Wildlife Agencies, unpublished report) suggested that because of the potential for raptors and corvids to use transmission line towers and distribution line poles as new perches and nest sites, placement of these facilities in seasonal sage-grouse habitats could impact the species through increased predation of adults, juveniles, and nests or result in sage-grouse abandoning sites (Knight and Kawashima 1993, Knight et al. 1995, Kochert and Olendorff 1999). The RCP identified as a priority conservation strategy the retrofitting of distribution line poles with perch deterrents to discourage raptors and corvids from perching. I evaluated the efficacy of five perch deterrents mounted on support poles of an 11-km section of a 12.5-kV distribution line that bisected the CA and habitat occupied by the sage-grouse population. Perch deterrents were mounted on the line in November-December 2006 following a random replicated block design that included controls. During 168 hours and 84 hours of direct observation in 2007 and 2008, respectively, I recorded 276 and 139 perching events of 7 potential avian predators of sage-grouse. Golden eagles (*Aquila chrysaetos*) were the dominant species recorded during both years. I did not detect any difference in perching events by perch deterrent we evaluated and controls ($p > 0.05$).

The effectiveness of perch deterrents evaluated may have been compromised by the structure of power poles and the basic design and placement of deterrents. The perch deterrents tested were partially successful in that they had the ability to prevent perching

on parts of the poles. However birds continued to perch on parts of the poles without deterrents, such as insulators. A perch deterrent that covers insulators, in combination with the physical deterrents tested, may increase the potential to prevent perching of avian predators on power poles of distribution lines.

The results of these studies will help update the information within the RCP and the SJCCP. The results can also be used by the Monticello/Dove Creek Local Working Group to plan future conservation activities within the CA. These studies provided a sound first step that can be built upon to improve habitat conditions within the CA and to reduce the threat of avian predation. Future work should take these results and expand them to larger scale projects.

LITERATURE CITED

Connelly, J.W., M.A. Schroeder, A.R. Sands, and C.E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Crawford, J.A., R.A. Olson, N.E. West, J.C. Mosley, M.A. Schroeder, T.D. Whitson, R.F. Miller, M.A. Gregg, and C.S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Gunnison Sage-grouse Rangewide Steering Committee. 2005. Gunnison Sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, USA.

Henderson, D.C., and M.A. Naeth. 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions 7:639-650.

Hull, A.C., and G.J. Klomp. 1967. Thickening and spread of crested wheatgrass stands

on southern Idaho ranges. Journal of Range Management 20:222-227.

Johnson, G.D., and M.S. Boyce. 1990. Feeding trials with insect in the diet of sage-grouse chicks. Journal of Wildlife Management 54:88-91.

Klott, J.H., and F.G. Lindzey. 1990. Brood habitat of sympatric sage grouse and Columbian Sharp-tailed grouse in Wyoming. Journal of Wildlife Management 54:84-88.

Knight, R.L., and J.Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear rights-of-ways. Journal of Wildlife Management 57: 266-271.

Knight, R.L., H.A.L. Knight, and R.J. Camp. 1995. Common Ravens and number and types of linear rights-of-way. Biological Conservation 4: 65-67.

Kochert, M.N., and R.R. Olendorff. 1999. Creating raptor benefits from power line problems. Journal of Raptor Research 33: 39-42.

Lupis, S.G. 2005. Summer ecology of Gunnison Sage-grouse (*Centrocercus minimus*) in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

Peterson, J.G. 1970. The food habits and summer distribution of juvenile sage-grouse in central Montana. Journal of Wildlife Management 34:147-155.

San Juan County Gunnison Sage-grouse Working Group (SWOG). 2000. Gunnison Sage-grouse Conservation Plan, San Juan County, Utah.

Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, MA. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and

S.J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363-376.

Schuman, G.E., F. Rauzi, and D.T. Booth. 1982. Production o Russian wildrye and crested wheatgrass and their effect on prairie soils. Agronomy Journal 74:23-26.

Sveum, C.M., J.A. Crawford, and W.D. Edge. 1998. Use and selection of brood-rearing habitats by sage-grouse in south central Washington. Great Basin Naturalist 58:344-351.

Wallestad, R.O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129-136.

Ward, S. 2007. Gunnison sage-grouse winter ecology and arthropod abundance diversity in relation to habitat use in San Juan County, Utah. Thesis, Utah State University, Logan, USA.

APPENDICES

Table A.1. Vegetation mixture seeded on Conservation Reserve Program (CRP) lands within the Gunnison Sage-grouse Conservation Area in San Juan County, Utah (SWOG 2000).

Species	PLS lbs/acre
Grasses	
Bluebunch wheatgrass	1.0
Thickspike wheatgrass	1.0
Western wheatgrass	1.5
Crested wheatgrass	0.5
Pubescent wheatgrass	1.0
Legumes/Forbs	
Alfalfa (Rambler)	1.0
Alfalfa (Ladak, Normad)	1.5
Western yarrow	0.12
Lewis flax	0.25
Sainfoin	0.5
Small burnet	2.0
Shrubs	
Wyoming big sagebrush	0.5
Forage kochia	0.5
Total	11.37

Table A.2. Shrubs, perennial grasses, annual grasses, and forbs measured in Conservation Reserve Program (CRP) and native sagebrush within the Gunnison Sage-grouse Conservation Study Area during the summers of 2007, 2008, and 2009. San Juan County, Utah.

		CRP plots	Sagebrush patches within CRP	Sagebrush plots
Perennial grass				
Crested wheatgrass	*Agropyron cristatum*	x	x	x
Blue grama	*Bouteloua gracilis*			x
Foxtail barley	*Hordeum jubatum*			x
Annual grass				
Cheat grass	*Bromus tectorum*	x	x	x
Forbs				
Russian knapweed	*Centaurea repens*	x		
Scaly globemallow	*Sphaeralcea leptophylla*		x	x
Goatsbeard	*Tragopogon dubius*	x		
Basin daisy	*Erigeron pulcherrimus*		x	x
Pale evening primrose	*Oenothera pallida*		x	x
Spreading daisy	*Erigeron divergens*		x	x
Cisco woody aster	*Xylorhia venusta*		x	x
African mustard	*Malcomia africana*	x	x	
Sulphur buckwheat	*Eriogonum umbellatum*		x	x
Vetch	*Astragalus* sp.			x
Heronsbill	*Erodium cicutarium*		x	x
Uinta groundsel	*Senecio multilobatus*			x
Russian thistle	*Salsola pestifer*	x		x
Common purslane	*Portulaca oleracea*			x
Hairy golden aster	*Heterotheca villosa*		x	x
Alfalfa	*Medicago polymorpha*	x		
Foothill deathcamas	*Zigadenus paniculatus*			x
Cryptantha	*Cryptantha* sp.		x	x
Rose-heath	*Leucelene ericoides*		x	x
Sub-shrub				
Broom snakeweed	*Gutierrezia sarothrae*		x	x
Shrubs				
Rubber rabbitbrush	*Chrysothamnus nauseosus*	x	x	x
Fringed sage	*Artemisia frigida*			x
Spineless horsebush	*Tetradymia canescens*			x
Wyoming big sage	*Artemisia tridentata* spp. wyomingensis		x	x

Table A.3. Tables reporting Type 3 tests of fixed effects and covariance parameter estimates of percent cover, height, and forage production of sagebrush, perennial grass, annual grass and forbs, and arthropod abundance in Conservation Reserve Program and native sagebrush plots for each water treatment (once a week, every 2 weeks, every 3 weeks) and grazing treatment (grazed, not grazed) in 2007, 2008, 2009, San Juan County, Utah ($p<0.001$).

A.3.1: Type 3 tests of fixed effects and covariance parameter estimates of forage production of perennial grasses, annual grasses, and forbs by Conservation Reserve Program and native sagebrush plots), water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2007, San Juan County, Utah (p<0.01).

		2007					
		Perennial grass		Annual grass		Forbs	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	0.03	0.87	0.51	0.50	11.64	0.01
Water	3,18	0.08	0.97	0.23	0.88	0.21	0.89
Habitat x water	3,18	0.23	0.87	0.26	0.85	0.42	0.74
Grazing	1,24	0.59	0.45	0.91	0.35	2.66	0.12
Habitat x grazing	1,24	4.48	0.05	0.91	0.35	0.46	0.50
Water x grazing	3,24	0.13	0.94	1.31	0.30	0.62	0.61
Habitat x water x grazing	3,24	0.42	0.74	4.14	0.02	0.3	0.83
		Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.000	.	0.001	0.001	0.000	.
Water x habitat		0.032	0.012	0.003	0.001	0.002	0.001
Water x grazing x habitat		0.000	.	0.000	.	0.000	.
Residual		0.018	0.005	0.002	0.001	0.004	0.001

A.3.2: Type 3 tests of fixed effects and covariance parameter estimates of forage production of perennial grasses, annual grasses, and forbs by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2008, San Juan County, Utah ($p<0.01$).

		2008					
		Perennial grass		Annual grass		Forbs	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	23.82	<0.01	2.17	0.19	12.03	0.01
Water	3,18	0.23	0.88	1.86	0.17	0.86	0.48
Habitat x water	3,18	1.38	0.28	4.1	0.02	0.1	0.96
Grazing	1,24	3.43	0.08	4.6	0.04	0.08	0.78
Habitat x grazing	1,24	0.12	0.73	1.79	0.19	0.44	0.51
Water x grazing	3,24	0.5	0.69	0.53	0.67	1.51	0.24
Habitat x water x grazing	3,24	0.55	0.65	0.65	0.59	0.33	0.81
		Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.004	0.003	0.003	0.002	0.000	.
Water x habitat		0.000	.	0.000	.	0.000	.
Water x grazing x habitat		0.000	.	0.000	.	0.000	0.001
Residual		0.013	0.003	0.007	0.002	0.006	0.000

A.3.3: Type 3 tests of fixed effects and covariance parameter estimates of forage production of perennial grasses, annual grasses, and forbs by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2009, San Juan County, Utah ($p<0.01$).

2009							
		Perennial grass		Annual grass		Forbs	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	12.37	0.01	0.49	0.51	13.12	0.01
Water	3,18	5.39	0.01	0.21	0.89	0.28	0.84
Habitat x water	3,18	0.55	0.65	1.96	0.16	1.74	0.20
Grazing	1,24	0.09	0.77	2.09	0.16	0.02	0.90
Habitat x grazing	1,24	12.51	0.00	0.67	0.42	0.76	0.39
Water x grazing	3,24	0.47	0.70	0.5	0.69	0.19	0.90
Habitat x water x grazing	3,24	0.55	0.65	0.55	0.65	0.57	0.64
		Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.007	0.006	0.002	0.002	0.002	0.002
Water x habitat		0.000	0.004	0.000	.	0.000	.
Water x grazing x habitat		0.000	.	0.000	.	0.000	.
Residual		0.018	0.005	0.005	0.001	0.008	0.002

A.3.4: Type 3 tests of fixed effects and covariance parameter estimates of percent cover of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2007, San Juan County, Utah ($p<0.01$).

		2007							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	3.06	0.13	1.99	0.21	3.6	0.11	67.67	<0.01
Water	3,18	0.86	0.48	1.12	0.37	0.47	0.71	0.41	0.75
Habitat x water	3,18	0.65	0.59	2.35	0.11	0.51	0.68	2.17	0.13
Grazing	1,24	0.58	0.45	2.19	0.15	0.6	0.45	6.6	0.02
Habitat x grazing	1,24	1.58	0.22	1.4	0.25	0.3	0.59	0.77	0.39
Water x grazing	3,24	0.33	0.80	0.74	0.54	0.39	0.76	0.67	0.58
Habitat x water x grazing	3,24	2.16	0.12	0.17	0.92	1.01	0.41	0.34	0.80
Time	1,48	1.77	0.19	8.67	0.01	72.59	<0.01	0.36	0.55
Habitat x time	1,48	0.71	0.40	7.72	0.01	11.97	<0.01	0.33	0.57
Water x time	3,48	1.11	0.35	0.93	0.43	2.16	0.11	0.5	0.68
Habitat x water x time	3,48	1.08	0.37	0.42	0.74	1.91	0.14	0.63	0.60
Grazing x time	1,48	0.66	0.42	1.96	0.17	0.75	0.39	0.34	0.56
Habitat x grazing x time	1,48	4.09	0.05	0.02	0.88	0.81	0.37	0.31	0.58
Water x grazing x time	3,48	0.57	0.64	0.12	0.95	0.32	0.81	0.46	0.71
Habitat x water x grazing x time	3,48	0.09	0.97	0.21	0.89	0.53	0.66	0.65	0.59
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.007	0.006	0.009	0.008	0.000	0.001	0.001	0.002
Water x habitat		0.002	0.005	0.004	0.006	0.001	0.003	0.004	0.004
Water x grazing x habitat		0.017	0.006	0.022	0.007	0.012	0.004	0.007	0.004
Residual		0.010	0.002	0.002	0.000	0.004	0.001	0.010	0.002

A.3.5: Type 3 tests of fixed effects and covariance parameter estimates of percent cover of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2008, San Juan County, Utah ($p<0.01$).

		2008							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	10.82	0.02	1.12	0.33	37.71	<0.01	86.6	<0.01
Water	3,18	0.58	0.64	2.26	0.12	0.33	0.81	0.06	0.98
Habitat x water	3,18	1.39	0.28	4.07	0.02	1.82	0.18	1.38	0.28
Grazing	1,24	0.3	0.59	4.38	0.05	1.34	0.26	1.44	0.24
Habitat x grazing	1,24	1.96	0.17	0.46	0.51	0.19	0.67	0.04	0.85
Water x grazing	3,24	0.13	0.94	0.12	0.95	0.43	0.74	0.23	0.87
Habitat x water x grazing	3,24	3.15	0.04	0.12	0.95	0.67	0.58	1.41	0.26
Time	1,48	0.06	0.80	11.88	<0.01	4.16	0.05	0.41	0.53
Habitat x time	1,48	1.32	0.26	0.06	0.81	7.97	0.01	0.12	0.73
Water x time	3,48	0.56	0.64	0.97	0.42	0.63	0.60	1.09	0.36
Habitat x water x time	3,48	0.2	0.89	2.3	0.09	0.53	0.67	0.93	0.43
Grazing x time	1,48	0.44	0.51	0.86	0.36	1.68	0.20	0.23	0.64
Habitat x grazing x time	1,48	0.03	0.87	0.01	0.91	0.23	0.63	0.11	0.74
Water x grazing x time	3,48	2.43	0.08	1.04	0.38	1.6	0.20	0.37	0.78
Habitat x water x grazing x time	3,48	0.53	0.67	0.21	0.89	0.87	0.46	0.59	0.62
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.003	0.004	0.017	0.014	0.000	0.001	0.000	.
Water x habitat		0.000	.	0.009	0.009	0.000	.	0.001	0.003
Water x grazing x habitat		0.016	0.005	0.022	0.009	0.006	0.002	0.009	0.004
Residual		0.010	0.002	0.016	0.003	0.006	0.001	0.006	0.001

A.3.6: Type 3 tests of fixed effects and covariance parameter estimates of percent cover of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2009, San Juan County, Utah (p<0.01).

		2009							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	24.8	<0.01	0.25	0.63	15.72	<0.01	43.73	<0.01
Water	3,18	0.15	0.93	3.93	0.03	0.17	0.91	1.31	0.30
Habitat x water	3,18	0.4	0.75	3.35	0.04	1.01	0.41	2.4	0.10
Grazing	1,24	0.11	0.74	1.55	0.23	1.56	0.22	2.25	0.15
Habitat x grazing	1,24	1.62	0.22	0	0.97	0.51	0.48	0.38	0.54
Water x grazing	3,24	1.52	0.24	2.39	0.09	0.7	0.56	0.68	0.57
Habitat x water x grazing	3,24	4.59	0.01	1.87	0.16	0.75	0.53	0.15	0.93
Time	1,48	4.29	0.04	0.75	0.39	0.5	0.48	2.9	0.10
Habitat x time	1,48	0.05	0.82	0.94	0.34	0.4	0.53	2.06	0.16
Water x time	3,48	1.01	0.40	0.4	0.75	1.04	0.38	2.63	0.06
Habitat x water x time	3,48	0.52	0.67	1.2	0.32	2.73	0.05	2.17	0.10
Grazing x time	1,48	0.43	0.52	0	0.95	0.17	0.68	0.25	0.62
Habitat x grazing x time	1,48	0.75	0.39	0	0.95	1.49	0.23	0.58	0.45
Water x grazing x time	3,48	1.18	0.33	2.03	0.12	1.25	0.30	0.06	0.98
IIabitat x watcr x grazing x time	3,48	2.26	0.09	1.35	0.27	0.82	0.49	0.16	0.92
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.000	.	0.003	0.003	0.000	0.001	0.004	0.004
Water x habitat		0.004	0.002	0.003	0.004	0.002	0.003	0.002	0.004
Water x grazing x habitat		0.000	.	0.006	0.004	0.007	0.003	0.009	0.005
Residual		0.017	0.003	0.011	0.002	0.005	0.001	0.015	0.003

A.3.7: Type 3 tests of fixed effects and covariance parameter estimates of height of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2007, San Juan County, Utah (p<0.01).

		2007							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	34.98	<0.01	1.54	0.26	1.06	0.34	77.38	<0.01
Water	3,18	1.72	0.20	2.58	0.09	0.38	0.77	0.49	0.69
Habitat x water	3,18	0.42	0.74	2.07	0.14	1.37	0.28	0.43	0.74
Grazing	1,24	1.34	0.26	1.07	0.31	2.75	0.11	2.97	0.10
Habitat x grazing	1,24	1.50	0.23	0.03	0.85	3.56	0.07	2.92	0.10
Water x grazing	3,24	0.10	0.96	0.48	0.70	0.24	0.87	0.81	0.50
Habitat x water x grazing	3,24	1.21	0.32	0.12	0.95	0.22	0.88	0.08	0.97
Time	1,48	19.38	<0.01	7.78	0.01	23.11	<0.01	0.72	0.40
Habitat x time	1,48	0.10	0.75	1.97	0.17	4.71	0.04	1.18	0.28
Water x time	3,48	0.25	0.86	2.30	0.09	1.08	0.37	0.82	0.49
Habitat x water x time	3,48	0.60	0.62	0.54	0.66	0.47	0.70	2.67	0.06
Grazing x time	1,48	1.57	0.22	1.08	0.30	0.34	0.56	0	0.95
Habitat x grazing x time	1,48	0.31	0.58	1.99	0.17	0.08	0.78	0.13	0.72
Water x grazing x time	3,48	2.02	0.12	1.14	0.34	1.18	0.33	0.35	0.79
Habitat x water x grazing x time	3,48	0.37	0.77	0.30	0.83	0.79	0.51	0.48	0.70
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.001	0.001	0.007	0.006	0.001	0.001	0.005	0.004
Water x habitat		0.000	.	0.004	0.003	0.000	.	0.000	.
Water x grazing x habitat		0.000	.	0.005	0.003	0.000	.	0.003	0.004
Residual		0.007	0.001	0.010	0.002	0.010	0.002	0.025	0.005

A.3.8: Type 3 tests of fixed effects and covariance parameter estimates of height of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2008, San Juan County, Utah ($p<0.01$).

		2008							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	12.56	0.01	0.38	0.56	48.33	<0.01	52.86	<0.01
Water	3,18	0.47	0.70	2.51	0.09	1.1	0.37	0.52	0.67
Habitat x water	3,18	0.48	0.70	2.91	0.06	0.29	0.83	0.25	0.86
Grazing	1,24	0.22	0.64	3.36	0.08	1.5	0.23	0.65	0.44
Habitat x grazing	1,24	6.37	0.02	0.08	0.78	4.37	0.05	2.85	0.10
Water x grazing	3,24	1.27	0.31	0.14	0.94	0.25	0.86	0.98	0.42
Habitat x water x grazing	3,24	1.55	0.23	0.03	0.99	1.14	0.35	0.39	0.76
Time	1,48	31.36	<0.01	17.45	<0.01	0.38	0.54	9.99	<0.01
Habitat x time	1,48	22.31	<0.01	0.57	0.45	0.12	0.73	0.6	0.44
Water x time	3,48	0.36	0.79	1.81	0.16	0.1	0.96	0.19	0.90
Habitat x water x time	3,48	1.79	0.16	1.63	0.19	0.48	0.70	1.12	0.35
Grazing x time	1,48	0.24	0.63	0.83	0.37	1.7	0.20	0.07	0.79
Habitat x grazing x time	1,48	1.39	0.24	1.08	0.30	0	0.98	0.39	0.53
Water x grazing x time	3,48	0.86	0.47	2.51	0.07	2.09	0.11	0.77	0.51
Habitat x water x grazing x time	3,48	2.04	0.12	0.08	0.97	3.24	0.03	0.93	0.43
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.002	0.002	0.005	0.004	0.000	0.000	0.004	0.006
Water x habitat		0.000	.	0.004	0.004	0.000	.	0.011	0.008
Water x grazing x habitat		0.006	0.002	0.010	0.004	0.002	0.001	0.018	0.006
Residual		0.004	0.001	0.005	0.001	0.004	0.001	0.006	0.001

A.3.9: Type 3 tests of fixed effects and covariance parameter estimates of height of perennial grasses, annual grasses, forbs, and sagebrush by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2009, San Juan County, Utah ($p<0.01$).

		2009							
		Perennial grass		Annual grass		Forbs		Sagebrush	
Effect	DF	*F*	*P*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat	1,6	14.66	0.01	0	0.98	8.82	0.03	31.12	<0.01
Water	3,18	1.4	0.27	6.29	<0.01	0.38	0.77	0.18	0.91
Habitat x water	3,18	0.09	0.97	4.04	0.02	2.47	0.10	0.33	0.81
Grazing	1,24	1.12	0.30	1.93	0.18	0.2	0.66	4.63	0.04
Habitat x grazing	1,24	12.61	<0.01	0.62	0.44	0.46	0.50	7.91	0.01
Water x grazing	3,24	0.64	0.60	0.67	0.58	0.04	0.99	1.91	0.16
Habitat x water x grazing	3,24	0.67	0.58	2.3	0.10	0.68	0.58	1.97	0.15
Time	1,48	17.16	<0.01	26.31	<0.01	0.21	0.65	11.00	<0.01
Habitat x time	1,48	0.21	0.65	1.47	0.23	1.16	0.29	11.00	<0.01
Water x time	3,48	1.23	0.31	0.6	0.62	2.14	0.11	1.03	0.39
Habitat x water x time	3,48	1.61	0.20	1.81	0.16	0.57	0.64	1.03	0.39
Grazing x time	1,48	0.08	0.78	1.03	0.32	0.33	0.57	0.00	0.99
Habitat x grazing x time	1,48	0.03	0.87	0.01	0.94	0.13	0.73	0.00	0.99
Water x grazing x time	3,48	0.49	0.69	1.46	0.24	1.07	0.37	0.43	0.74
Habitat x water x grazing x time	3,48	0.13	0.94	0.23	0.88	0.79	0.50	0.43	0.74
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Habitat		0.002	0.002	0.003	0.002	0.000	0.001	0.013	0.010
Water x habitat		0.002	0.002	0.002	0.001	0.002	0.001	0.008	0.007
Water x grazing x habitat		0.000	0.001	0.002	0.001	0.001	0.001	0.021	0.006
Residual		0.007	0.001	0.005	0.001	0.003	0.001	0.002	0.000

A.3.10: Type 3 tests of fixed effects arthropod orders by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2007, San Juan County, Utah (p<0.01).

		2007									
		Aranae		Coleoptera		Diptera		Hemiptera		Homoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*	*F*	*p*
Habitat	1,6	8.10	0.03	1.46	0.27	23.40	<0.01	2.33	0.18	0.20	0.67
Water	3,18	1.12	0.37	0.22	0.88	0.17	0.91	1.29	0.31	0.35	0.79
Habitat x water	3,18	0.06	0.98	0.38	0.77	1.73	0.20	0.67	0.58	2.29	0.11
Grazing	1,24	0.11	0.75	6.80	0.04	0.07	0.81	1.12	0.33	2.17	0.19
Habitat x grazing	1,24	0.00	0.95	0.00	0.97	0.71	0.43	1.38	0.28	0.00	0.97
Water x grazing	3,24	0.31	0.82	0.76	0.53	1.75	0.19	1.16	0.35	0.58	0.64
Habitat x water x grazing	3,24	0.07	0.98	0.86	0.48	0.24	0.87	2.03	0.15	1.10	0.37

		Hymenoptera (ants)		Hymenoptera (bees and wasps)		Lepidoptera		Orthoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*
Habitat	1,6	0.17	0.70	2.85	0.14	1.02	0.35	45.4	<0.01
Water	3,18	1.03	0.40	0.79	0.52	0.21	0.89	0.25	0.86
Habitat x water	3,18	3.44	0.04	1.86	0.17	0.37	0.78	0.17	0.92
Grazing	1,24	0.59	0.48	0.16	0.70	0.47	0.52	0.06	0.82
Habitat x grazing	1,24	0.52	0.50	0.48	0.51	3.31	0.12	0.11	0.75
Water x grazing	3,24	1.39	0.28	0.53	0.67	0.68	0.57	0.52	0.67
Habitat x water x grazing	3,24	0.02	0.99	1.79	0.19	1.20	0.34	1.61	0.22

A.3.11: Type 3 tests of fixed effects arthropod orders by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2008, San Juan County, Utah ($p<0.01$).

		2008									
		Aranae		Coleoptera		Diptera		Hemiptera		Homoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*	*F*	*p*
Habitat	1,6	1.49	0.27	3.61	0.11	0.04	0.85	10.7	0.02	23.9	<0.01
Water	3,18	0.49	0.69	0.68	0.58	2.01	0.15	3.26	0.05	3.36	0.04
Habitat x water	3,18	0.55	0.66	0.75	0.54	0.71	0.56	4.75	0.01	2.26	0.12
Grazing	1,24	0.23	0.65	7.22	0.04	0.55	0.49	0.96	0.37	6.52	0.04
Habitat x grazing	1,24	1.61	0.25	2.08	0.20	1.88	0.22	1.27	0.30	7.65	0.03
Water x grazing	3,24	1.06	0.39	2.20	0.12	1.37	0.29	1.60	0.22	3.94	0.03
Habitat x water x grazing	3,24	1.85	0.17	2.22	0.12	2.01	0.15	2.52	0.09	2.75	0.07

		Hymenoptera (ants)		Hymenoptera (bees and wasps)		Lepidoptera		Orthoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*
Habitat	1,6	0.09	0.78	0.01	0.94	14.4	0.01	108	<0.01
Water	3,18	0.76	0.53	0.35	0.79	0.42	0.74	0.28	0.84
Habitat x water	3,18	0.77	0.53	3.59	0.03	1.31	0.30	2.85	0.07
Grazing	1,24	3.50	0.11	0.80	0.40	0.45	0.53	0.32	0.59
Habitat x grazing	1,24	1.26	0.30	0.02	0.91	0.22	0.65	0.04	0.84
Water x grazing	3,24	1.70	0.20	2.07	0.14	3.48	0.04	0.72	0.55
Habitat x water x grazing	3,24	0.92	0.45	2.97	0.06	1.05	0.39	0.92	0.45

A.3.12: Type 3 tests of fixed effects arthropod orders by Conservation Reserve Program and native sagebrush plots, water treatment (once a week, every 2 weeks, every 3 weeks), and grazing treatment (grazed, not grazed) in 2009, San Juan County, Utah ($p<0.01$).

		2009									
		Aranae		Coleoptera		Diptera		Hemiptera		Homoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*	*F*	*p*
Habitat	1,6	4.23	0.09	0.00	0.99	1.04	0.35	6.10	0.05	0.60	0.47
Water	3,18	0.46	0.72	1.28	0.31	0.60	0.63	2.50	0.09	2.49	0.09
Habitat x water	3,18	1.00	0.42	1.11	0.37	1.31	0.30	2.10	0.14	3.12	0.05
Grazing	1,24	0.94	0.37	0.45	0.53	0.03	0.88	0.13	0.73	2.57	0.16
Habitat x grazing	1,24	1.29	0.30	0.42	0.54	0.05	0.83	0.00	0.97	0.08	0.79
Water x grazing	3,24	1.16	0.35	0.89	0.47	0.75	0.54	0.58	0.64	0.99	0.42
Habitat x water x grazing	3,24	1.62	0.22	0.48	0.70	1.25	0.32	0.66	0.59	3.15	0.05

		Hymenoptera (ants)		Hymenoptera (bees and wasps)		Lepidoptera		Orthoptera	
Effect	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*P*
Habitat	1,6	0.15	0.71	0.48	0.52	3.95	0.09	83.6	<0.01
Water	3,18	0.82	0.50	0.27	0.84	1.18	0.35	0.55	0.65
Habitat x water	3,18	0.70	0.56	3.66	0.03	0.09	0.96	0.24	0.87
Grazing	1,24	1.11	0.33	0.47	0.52	1.20	0.32	0.32	0.59
Habitat x grazing	1,24	3.57	0.11	0.10	0.76	1.20	0.32	0.03	0.87
Water x grazing	3,24	0.59	0.63	0.87	0.48	2.20	0.12	3.34	0.04
Habitat x water x grazing	3,24	0.40	0.76	0.36	0.78	0.20	0.90	0.28	0.84

A.4. Copyright release letters of the *Journal of Wildlife Management* and Allen Press allowing the republication of: Prather, P.R. and T.A. Messmer. 2010. Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah. *Journal of Wildlife Management* 74(4): 796-800.

allen press™
PUBLISHING SERVICES

April 22, 2010

Dear Phoebe Prather,

On behalf of the Allen Press Publishing Services, I am pleased to grant permission to you for the reprinting of the following:

Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah. *Journal of Wildlife Management.* 74.4.

For use in a Dissertation.

This permission is a one-time, non-exclusive, electronic worldwide grant for English language use as described in this letter, and is subject to the following conditions:

1. No payment is required.
2. Each copy containing our material that you reproduce or distribute must bear the appropriate copyright information, crediting the author, journal, and publisher (The Wildlife Society, Allen Press Publishing Services).
3. The original author's permission must also be independently obtained before permission is granted.

If these terms are acceptable, please sign and date, and fax back to my attention at 785-843-1853. This permission will be effective upon our receipt of the signed contract. If applicable, when sending payment, please make clear reference to our title and author. Materials should be addressed to *Journal of Wildlife Management*, c/o Valerie Pierce/APPS, P.O. Box 7052, Lawrence, KS 66044.

Sincerely,

Valerie Pierce
Publishing Coordinator
Allen Press Publishing Services

AGREED: _____ DATE: 26 April 2010

_____ We have elected not to use this material

Date: 26 April 2010

Name: Phoebe Prather
Address: 255 South 400 East Logan, UT 84321
Phone/e-mail address: (508)776-2281/phoebe.prather@usu.edu

Journal Name: The Journal of Wildlife Management
Journal Address: 202 Natural Resources, University of Missouri Columbia, MO 65211-7260

To Permissions Editor:

I am preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete my degree in the summer of 2010.

An article, Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah, of which I am first author, and which will appear in your journal May, 2010, Vol. 74, Issue 4, reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation. (Reprinting the chapter may necessitate some revision.) Please note that USU sends dissertations to Bell & Howell Dissertation Services to be made available for reproduction.

I will include an acknowledgment to the article on the first page of the chapter, as shown below. Copyright and permission information will be included in a special appendix. If you would like a different acknowledgment, please so indicate.

Please indicate your approval of this request by signing in the space provided, and attach any other form necessary to confirm permission. If you charge a reprint fee for use of an article by the author, please indicate that as well.

If you have any questions, please call me at the number above or send me an e-mail message at the above address. Thank you for your assistance.

Phoebe Prather

I hereby give permission to Phoebe Prather to reprint the requested article in her dissertation, with the following acknowledgment:

(Acknowledgment, including full bibliographical information, including title, journal, volume, date, and page numbers)

Signed Valerie D. Rowe

Date 4/26/2010

Fee $0.00

CURRICULUM VITAE

Phoebe R. Prather

(May 2010)

CARREER OBJECTIVE:

To obtain a position with an organization that requires technical expertise and communication skills. Special areas of interest: habitat management, habitat restoration, and avian, wetland and riparian ecology and management.

EDUCATION:

B.A. in Environmental Studies, University of California at Santa Cruz, Santa Cruz, California. (06/2002). Emphasis in environmental policy and land management. Received honors on undergraduate thesis. Ph.D. in Ecology, Utah State University, Logan, Utah. (expected 07/2010). Grad GPA: 3.63. Dissertation research in Utah 2006-2009.

EXPERIENCE:

GRADUATE RESEARCH ASSISTANT, Utah State University, Ph.D. Candidate in Ecology, Logan, Utah (06/2006-05/2010).

- Designed, implemented, and analyzed statistically valid field experiments to address conservation strategies identified in the San Juan County, Utah Gunnison Sage-grouse Conservation Plan. Collected, compiled, organized and analyzed field data, and presented the results in both written and oral formats.
- Communicated, collaborated and formed relationships with state and federal agencies, non-profit organizations, and private landowners.
- Supervised field technicians and Youth Conservation Corp work crews.

- Surveyed raptor and corvid use of distribution line power poles fitted with perch deterrents.
- Created wet meadow brood-rearing habitats in sagebrush habitats and Conservation Reserve Program fields through the use of irrigation.
- Proficient in diverse vegetation measurement techniques and methodologies.
- Trapped arthropods using pit-fall traps and sorted them to family using a dissecting scope and dichotomous key.
- Prepared and edited annual reports.
- Presented results at stakeholder conferences and professional meetings to diverse audiences.

RESEARCH ASSISTANT, Delta Waterfowl Foundation, Minnedosa Field Station, Manitoba, Canada (04/2005-08/2005).

- Conducted research on nesting mallard hens. Trapped hens using decoy traps, Weller traps, and nesting tunnel traps. Banded, took measurements, collected feathers, and placed nasal markers on captured hens. Maintained a field notebook and field datasheets.
- Nest searched using ATV's and a drag chain.
- Monitored nests of several upland nesting waterfowl species.
- Used the candling technique to age eggs.
- Banded mallard ducklings using plastacine bands.
- Re-sighted Mallard hens with nasal markers using a spotting scope.

- Assisted other graduate student crews based out of the field station conducting research on American Coots, Ruddy Ducks, and Stripped Skunks. Became familiar with radio-telemetry techniques while assisting the skunk crew.

ENDANGERED SHOREBIRD MONITOR AND NATURALIST, Massachusetts Audubon Society, Cummaquid, MA (04/2004-09/2004).

- Worked at the Mass Audubon Sampson's Island/Dead Neck Wildlife Sanctuary, Cape Cod.
- Monitored nesting Piping Plovers. Visited island daily to determine breeding territories. Fenced off territories and posted signs. Constructed predator exclosures around nests. Intensely monitored broods, keeping a record of number of chicks hatched and fledged. Completed daily observation forms.
- Monitored Least and Common Tern nesting colonies. Fenced off nesting colonies. Conducted weekly counts of nests. Constructed and maintained a solar powered electric predator fence.
- Researched, prepared, and conducted weekend nature walks for groups of 2 to 20 people of all ages.
- Conversed with visitors, checked Audubon memberships, sold memberships, collected day fees, and provided information on nesting birds and the methods taken to protect them.
- Used a 13 foot Boston Whaler to reach and patrol the island.

- Volunteered with Massachusetts Fish and Wildlife to conduct Roseate Tern nesting surveys and assist in banding and weighing Common and Roseate Tern chicks.
- Volunteered with Monomoy National Wildlife Refuge to conduct Herring and Great Black-backed Gull nesting survey and to conduct Horseshoe Crab surveys twice a month on night full and new moon tides.
- Supervised high school student volunteers.

RESOURCE ASSISTANT, Student Conservation Association, Arches National Park, Interpretation Division, Moab, Utah (07/2003-10/2003).

- Researched, composed, and presented an evening slideshow program on the natural histories of raptors for an audience of up to 70 people.
- Researched, prepared, and conducted guided hikes and nature walks for groups of up to 30 people.
- Staffed park visitor desk, provided park and area information, aided visitors in trip planning, responsible for the handling of fees, selling tour tickets, reconciling funds, and completing associated paperwork.
- Educated visitors on the desert ecosystems and the challenges that they face.
- Aided in search and rescue incidents.

RESOURCE ASSISTANT, Student Conservation Association, Arches National Park, Resource Management Division, Moab, Utah (03/2003-07/2003).

- Monitored raptor nests of eight species of birds prey, including determining activity and counting number of young and fledged young at 70 historic nesting sites.
- Monitored a Great-Blue Heron Rookery on the Colorado River throughout the nesting season.
- Conducted a weekly Breeding Bird Survey identifying songbirds of the pinyon-juniper habitat by sight and song.
- Assisted researchers in vegetation transects and riparian bird point count surveys.
- Assisted in boundary fencing projects and rehabilitation of areas damaged by off-road vehicle use.
- Researched and composed the life histories for the raptor and songbird species surveyed.
- Used a four-wheel drive vehicle and hiking in extreme summer desert conditions to reach the nest sites.
- Prepared and edited seasonal reports.
- Aided in search and rescue incidents.

INTERNSHIP, Alaska Audubon Society, Anchorage, Alaska (10/2002-12/2002).

- Aided in the development of the Alaska State Important Bird Area (IBA) program.
- Entered data into the World Bird Database for over 200 Important Bird Areas in the Cook Inlet watershed and along the Bering Sea coast.

- Designed criteria for passerine Important Bird Areas with U.S. Fish and Wildlife biologists.
- Researched and prepared a pamphlet aiming to educate the public on the IBA program.
- Researched and composed the life histories for bird species on the Audubon Alaska Watch List.

BIRD BANDER, Denali Institute, Denali National Park, Alaska (07/2002-09/2002).

- Operated a passerine bird banding station in the heart of Denali National Park at the Denali Institute Migration Station.
- Utilized and maintained 10 nets; banded 7 days a week; recorded specific data on each individual.
- Presented an evening program to 20 to 40 lodge guests and conducted hands-on demonstrations for the guests at the banding station.

AWARDS AND HONORS:

- Received Honors on undergraduate thesis entitled, "What the Heck in as IBA: A case study of the Important Bird Area Program in the Owens Valley, California," from the University of California at Santa Cruz in 2002.
- Recipient of the Utah Chapter of the Wildlife Society Annual Scholarship in 2007.

PROFESSIONAL PRESENTATIONS:

- Prather, Phoebe R. and T.A. Messmer. 2006. "Use of Artificial Wet Meadow Areas by Gunnison Sage-grouse (*Centrocercus minimus*) in San Juan County,

Utah." Presented at The Utah Chapter of the Wildlife Society Annual Conference in Moab, UT.

- Prather, Phoebe R. and T.A. Messmer. 2007. "Raptor and Corvid Use of Distribution Line Power Poles: An Assessment of the Efficacy of Perch Deterrents." Presented at The Utah Chapter of the Wildlife Society Annual Conference in Moab, UT.
- Prather, Phoebe R. and T.A. Messmer. 2007. "Raptor and Corvid Use of Distribution Line Power Poles: An Assessment of the Efficacy of Perch Deterrents." Presented at The Utah Sage-grouse Summit in Salt Lake City, UT.
- Prather, Phoebe R. and T.A. Messmer. 2008. "Raptor and Corvid Use of Distribution Line Power Poles: An Assessment of the Efficacy of Perch Deterrents." Presented at The Gunnison Sage-grouse Summit in Montrose, CO.
- Prather, Phoebe R. and T.A. Messmer. 2008. "Raptor and Corvid Use of Distribution Line Power Poles: An Assessment of the Efficacy of Perch Deterrents." Presented at The Western Association of Fish and Wildlife Agencies Sage-grouse and Sharp-tailed Grouse Conference in Mammoth Lakes, CA.

RESEARCH PUBLICATIONS AND REPORTS:

- Prather, Phoebe R. and T.A. Messmer. 2007. Annual Report. "Gunnison Sage-grouse (*Centrocercus minimus*) Conservation in Utah: A summary of species and habitat response to conservation strategies identified in the Gunnison Sage-grouse Rangewide Conservation Plan." Department of Wildland Resources, Utah State University, Logan, UT.

- Prather, Phoebe R. and T.A. Messmer. 2008. Annual Report. "Gunnison Sage-grouse (*Centrocercus minimus*) Conservation in Utah: A summary of species and habitat response to conservation strategies identified in the Gunnison Sage-grouse Rangewide Conservation Plan." Department of Wildland Resources, Utah State University, Logan, UT.
- Prather, Phoebe R. and T.A. Messmer. 2009. Annual Report. "Gunnison Sage-grouse (*Centrocercus minimus*) Conservation in Utah: A summary of species and habitat response to conservation strategies identified in the Gunnison Sage-grouse Rangewide Conservation Plan." Department of Wildland Resources, Utah State University, Logan, UT.
- Prather, P.R. and T.A. Messmer. In press. "Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah." *Journal of Wildlife Management.*

PROFESSIONAL MEMBERSHIPS:

The Wildlife Society

Utah Chapter of the Wildlife Society

Journal of Applied Ecology 2013 doi: 10.1111/1365-2664.12097

Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems

Michael D. Reisner[1]*†, James B. Grace[2], David A. Pyke[3] and Paul S. Doescher[4]

[1]*Department of Environmental Studies, Augustana College, Rock Island, IL 61201, USA;* [2]*US Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, LA 70506, USA;* [3]*US Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA; and* [4]*Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA*

Summary

1. Ecosystem invasibility is determined by combinations of environmental variables, invader attributes, disturbance regimes, competitive abilities of resident species and evolutionary history between residents and disturbance regimes. Understanding the relative importance of each factor is critical to limiting future invasions and restoring ecosystems.

2. We investigated factors potentially controlling *Bromus tectorum* invasions into *Artemisia tridentata* ssp. *wyomingensis* communities across 75 sites in the Great Basin. We measured soil texture, cattle grazing intensity, gaps among perennial plants and plant cover including *B. tectorum*, biological soil crusts (BSCs) and bare soil. Using *a priori* knowledge, we developed a multivariate hypothesis of the susceptibility of *Artemisia* ecosystems to *B. tectorum* invasion and used the model to assess the relative importance of the factors driving the magnitude of such invasions.

3. Model results imply that bunchgrass community structure, abundance and composition, along with BSC cover, play important roles in controlling *B. tectorum* dominance. Evidence suggests abundant bunchgrasses limit invasions by limiting the size and connectivity of gaps between vegetation, and BSCs appear to limit invasions within gaps. Results also suggest that cattle grazing reduces invasion resistance by decreasing bunchgrass abundance, shifting bunchgrass composition, and thereby increasing connectivity of gaps between perennial plants while trampling further reduces resistance by reducing BSC.

4. *Synthesis and applications*. Grazing exacerbates *Bromus tectorum* dominance in one of North America's most endangered ecosystems by adversely impacting key mechanisms mediating resistance to invasion. If the goal is to conserve and restore resistance of these systems, managers should consider maintaining or restoring: (i) high bunchgrass cover and structure characterized by spatially dispersed bunchgrasses and small gaps between them; (ii) a diverse assemblage of bunchgrass species to maximize competitive interactions with *B. tectorum* in time and space; and (iii) biological soil crusts to limit *B. tectorum* establishment. Passive restoration by reducing cumulative cattle grazing may be one of the most effective means of achieving these three goals.

Key-words: bare ground, biological soil crusts, cattle grazing, disturbance, diversity, invasion, plant gaps

Introduction

Ecosystem invasibility is governed by a complex collection of biotic and abiotic factors including environmental conditions, disturbance regimes and responses of native species to those regimes, as well as the biotic resistance provided by the resident community (Lonsdale 1999; Richardson & Pysek 2006). Biotic resistance is especially important in limiting the magnitude of invasive species after they have established (Levine, Adler & Yelenik 2004). Changes that increase resource availability are likely to increase susceptibility to invasion (Davis, Grime & Thompson 2000). Further, the introduction of an exotic herbivore with which resident species have no

†Present address: Environmental Studies Department, Augustana College, Rock Island, IL 61201, USA.
*Corresponence author. E-mail: michaelreisner@augustana.edu

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society

evolutionary history may exacerbate the magnitude of non-native plant invasions if it reduces the competitive abilities of native plants and increases resource availability (Parker, Burkepile & Hay 2006). Developing a predictive understanding of invasibility requires that we develop an understanding of how the various factors work together to limit invasion (Agrawal *et al*. 2007).

Artemisia tridentata big sagebrush ecosystems of the Intermountain West, USA, evolved with little herbivore pressure until the introduction of livestock (Mack & Thompson 1982). Within these ecosystems, lower elevation, more arid, *A. tridentata* ssp. *wyomingensis* (henceforth *Artemisia*) communities are the most common, but least resistant to invasion by exotic annual plants and least resilient to disturbance (Miller *et al*. 2011). Even in the absence of fire, these communities are especially vulnerable to invasions by *Bromus tectorum* L, and under some circumstances, *B. tectorum* can dominate the herbaceous understorey community (Miller *et al*. 2011). Previous studies have demonstrated the importance of several factors in the invasion process (soil texture, landscape orientation, competition-driven biotic resistance from native bunchgrasses and biological soil crust (BSC) communities (Table 1). Livestock grazing has been implicated in the spread and dominance of *B. tectorum* via several mechanisms (Mack & Thompson 1982; Table 1). Nonetheless, we have a poor understanding of how these factors work together and their relative importance in determining the magnitude of *B. tectorum* invasions (Miller *et al*. 2011).

Once *B. tectorum* sufficiently dominates the understorey and fills interspaces among plants, it creates a continuous, highly flammable fuel that significantly increases the risk of fire (Pyke 2011). Once a fire occurs, *B. tectorum* increases the frequency of fires. This change in fire regime may lead to a 'catastrophic regime shifts' (Scheffer *et al*. 2009), whereby native shrub–steppe communities are transformed into annual grasslands dominated by *B. tectorum* and other invasives (Miller *et al*. 2011). For practical purposes, these shifts are irreversible because of the significant investments necessary to restore these systems (Pyke 2011).

Preventing such regime shifts will require a better understanding of the simultaneous interacting factors that determine the magnitude of *B. tectorum* invasion once it has established in pre-fire *Artemisia* communities (Miller *et al*. 2011). Managers would benefit from understanding the causal network of mechanisms by which these factors interact with each other and how they collectively influence *B. tectorum* dominance. They would also benefit from an early warning indicator that the cumulative resistance of the resident community has been compromised to the point that *B. tectorum* likely dominates the understorey and thereby potentially setting the stage for a regime shift with the next fire.

Using *a priori* knowledge, we developed a multivariate hypothesis of the invasibility of *Artemisia* ecosystems to *B. tectorum* invasion in the absence of fire based upon the findings of previous studies in this system. The model included abiotic (soil physical properties, landscape orientation), cattle grazing disturbance and biotic factors (resident community abundance, composition and structure), predicted to be important determinants of *B. tectorum* dominance (Fig. 1, Table 1). Our analyses addressed the following questions: (i) What combination of abiotic and biotic conditions limit the magnitude of *B. tectorum* dominance? (ii) Can shifts in community structure, measured by the size and connectivity of gaps between native plants, serve as an indicator of susceptibility to *B. tectorum*

Table 1. Components of hypothesis represented by initial metamodel (Fig. 1)

Path	Hypothesized mechanism
1	(−) Cattle herbivory decreases *Bromus tectorum* abundance (Hempy-Mayer & Pyke 2009). (+) Cattle increase abundance by dispersing seeds and increasing propagule pressure (Schiffman 1997)
2	Cattle trampling decreases biological soil crusts cover and increases safe sites for *B. tectorum* establishment (Ponzetti, McCune & Pyke 2007)
3	Cattle herbivory decreases bunchgrass abundance (Briske & Richards 1995)
4	Cattle herbivory alters bunchgrass community composition by favouring more grazing-resistant species (Briske & Richards 1995)
5	Higher heat loads and spring insolation increase *B. tectorum* abundance (Stewart & Hull 1949; Chambers *et al*. 2007)
6	Lower heat loads increase bunchgrass productivity (Davies, Bates & Miller 2007)
7	Deeper, coarser-textured soils increase *B. tectorum* abundance (Stewart & Hull 1949)
8	Changes in bunchgrass composition influence community structure because species have different life forms (Grime 1977; James *et al*. 2008)
9	Changes in bunchgrass composition influence invasibility because species have different competitive abilities (Goldberg & Barton 1992) and patterns of resource use (James *et al*. 2008)
10	Bunchgrass abundance is inversely related to the size of and connectivity between gaps in perennial vegetation (Herrick *et al*. 2005)
11	Native bunchgrass abundance decreases *B. tectorum* abundance by reducing resource availability (Chambers *et al*. 2007)
12	Safe sites increase *B. tectorum* establishment rates (Fowler 1988).
13	Sagebrush abundance may increase *B. tectorum* abundance via facilitation (Griffith 2010) or decrease abundance via competition (Reichenberger & Pyke 1990).
14	Increases in the size of and connectivity between gaps in perennial vegetation increase *B. tectorum* abundance by increasing general resource availability (James *et al*. 2008; Okin *et al*. 2009)

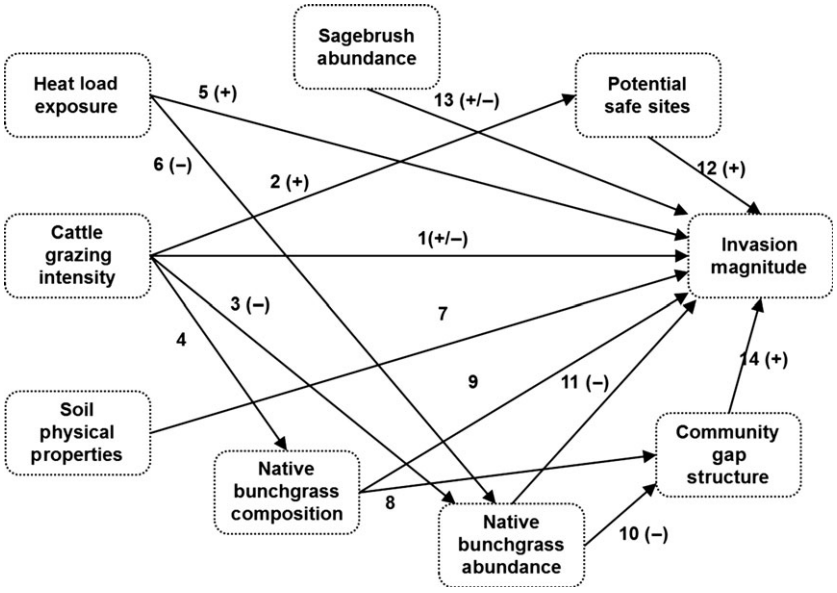


Fig. 1. Conceptual *a priori* multivariate model of *Artemisia* ecosystem susceptibility to *Bromus tectorum* dominance in the absence of fire. Dotted-line boxes represent conceptual variables hypothesized to influence invasibility. Components of the overall hypothesis are described in Table 1.

dominance and thereby vulnerability to a regime shift with the next fire?

We used structural equation modelling (SEM) to evaluate a multivariate hypothesis across 75 sites already invaded by *B. tectorum*. SEM provides a means of representing complex hypotheses about causal networks and testing for model data consistency (Grace 2006). It represents an advance over classical regression approaches (e.g. multiple regression) when used with observational data (Grace, Youngblood & Scheiner 2009). The advance provided by SEM comes partially from incorporating the associations among predictors into the overall hypothesis rather than to simply ignore or control for them. This is accomplished by extending the univariate model ($y = a + \beta x + \varepsilon$) to allow ys to depend on other ys and thereby represent networks of relationships in SEMs ($y = a + \beta x + \gamma y + \varepsilon$).

Because of this capability, SEM models can be used to specify hypotheses about mediating pathways and address questions, such as Can an association between A and C be explained by the factor B? This is achieved by evaluating a model such as $A \rightarrow B \rightarrow C$ and determining whether or not $r_{AC} = r_{AB} \cdot r_{BC}$. By assuming (and justifying based on prior information) that if A were manipulated, B could show a response, and similarly, if B were manipulated, C could show a response, then a test of the conditional independence of A and C in our example ($A \perp C|B$) could permit a result leading us to reject that possibility (A not independent of C when conditioned on B). SEMs thus build on causal assumptions to yield testable implications that can be evaluated with data. Estimated parameters obtained for a selected model then represent a set of predictions for further testing. The ultimate test of an SEM model is its ability to correctly predict future samples. For individual applications, the plausibility of causal assumptions (e.g. previous demonstrations that varying A can lead to response in B or known mechanisms whereby A can influence B) is often sufficient for reasonable inferences to be made.

Our results suggest that bunchgrass community structure, abundance and composition, and BSCs all play critical roles in limiting the magnitude of *B. tectorum* dominance. Cattle grazing may exacerbate the magnitude of invasion by reducing biotic resistance. Model evaluations imply that cattle grazing can reduce bunchgrass cover and shift bunchgrass community composition towards grazing-tolerant species and thereby increase the size and connectivity of gaps among perennial vegetation exacerbating invasion. Cattle trampling may also exacerbate invasion by reducing BSC cover. Ultimately, increases in the size and connectivity of gaps among native perennial vegetation may provide managers with an early warning indicator of increased susceptibility to *B. tectorum* dominance of *Artemisia* communities and thereby increased vulnerability to regime shifts in one of North America's most widespread but endangered ecosystems.

Materials and methods

STUDY AREA AND SAMPLING DESIGN

The study examined 75 *Artemisia* sites scattered across 4700 km^2 (roughly the size of state of Rhode Island) with elevations between 1265 and 1580 m across five *Artemisia*-dominated plant associations of the northern Great Basin floristic province of Oregon, USA. Natural Resource Conservation Service (NRCS) Ecological Site Descriptions and digital soil maps (http://websoilsurvey.nrcs.usda.gov) were used to ensure coverage of spatial variation in water stress driven by soil texture. Plant communities varied in dominant perennial tussock grasses and included the following ecological sites (ES): (i) loamy 254–308 mm precipitation zone (PZ) with *Pseudoroegneria spicata* and *Achnatherum thurberianum*; (ii) sandy loam 203–254 mm PZ with *Hesperostipa comata* and *P. spicata*; (iii) clayey 254–308 mm PZ with *A. thurberianum* and *Poa secunda*; and (iv and v) north slopes and south slopes 152–254 mm PZ with *P. spicata* and *A. thurberianum* co-dominating north and south slopes, respectively.

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society, *Journal of Applied Ecology*

Each ES was delineated into three landscape substrata using 10-m resolution US Geological Survey Digital Elevation Models (DEM) to ensure variation in heat loads and water stress associated with changes in landscape orientation: (i) northerly aspects (0–90°, 270–360°), (ii) southerly aspects (90–270°) or (iii) flat. Study plots were located at different distances from the nearest livestock watering locations to capture variation in cattle grazing intensity. Random points were selected and field verified to ensure that plots were located: (i) every 200–400 m, starting at 100 m and extending to >3200 m from the nearest water; (ii) in as many soil–landscape strata combinations as possible; and (iii) >200 m from the nearest road to minimize related effects. To reduce potential confounding effects of time since fire, all sites burned since 1930 were excluded using a fire perimeter data base (http://sagemap.wr.usgs.gov accessed 17/3/2008).

SAMPLING

Thirty of the 0·39-ha study plots were sampled in 2008 and another 45 in 2009. Six 25-m transects were established in each plot using a spoke design, and herbaceous, shrub and BSC cover measured using line–point intercept (Herrick *et al.* 2005). All sampling occurred between 10 May and 15 July in both years to capture peak herbaceous biomass. Aspect and slope of each plot were calculated from DEM using Arc-GIS 13·0 and, with latitude, used to calculate potential heat loads for each plot (McCune 2007).

Potential variation in water stress was inferred by the following measurements: (i) soil texture at 0–15 cm soil depth; (ii) potential effective rooting depth, which was measured by digging a soil pit until bedrock, a restrictive layer (clay accumulation layer) or 2 m depth was reached; and (iii) amount and timing of precipitation for each study site derived from PRISM at 2-km^2 cell resolution (Daly *et al.* 2008). Sampling-year precipitation for all study plots was estimated for three seasons: 1 August to 31 October (fall), 1 November to 31 March (winter) and 1 April to 31 July (spring–summer).

Cattle grazing intensity was quantified by four measurements: field-verified distance from the nearest water; dung frequency and dung density from 12, 1 × 25 m belt transects; and bunchgrass (tussock) basal area. Basal circumference (C) of 30 randomly selected bunchgrasses was measured in each plot and used to calculate bunchgrass basal area (cm^2) using the following formula: Area = $\pi\,(C/2\pi)^2$.

Bare soil cover was calculated using line–point intercept data to represent exposed soil surface not covered by vegetation, visible BSC, dead vegetation, litter or rocks (Herrick *et al.* 2005). Soil surface aggregate stability was assessed in interspace microsites at 18 random sampling points along transects using soil from the upper 0–4 mm (Herrick *et al.* 2005). Two indicators of soil erosion resistance were calculated: mean soil stability and proportion of samples rated as extremely stable (Beever, Huso & Pyke 2006).

We assessed the structure of the native perennial community by quantifying the size of and connectivity of gaps between such vegetation using the basal gap intercept method (Herrick *et al.* 2005). We calculated mean gap length and the proportion of transects covered by large gaps (>200 cm in length).

MULTIVARIATE ANALYSIS

Species cover, distance from nearest water, dung density, bunchgrass basal area, heat loads, soil depth, precipitation, gap size and herbaceous biomass data were log-transformed to improve distributional properties, correlations with ordination axes and variation explained by ordinations (McCune & Grace 2002). Other variables were not transformed.

Non-metric multidimensional scaling (NMS) ordination was used to relate patterns in community composition to environmental gradients (PC-Ord™; McCune & Grace 2002). Joint plots and Pierson's correlations were used to describe relationships between environmental gradients and the strongest patterns of community composition.

We used nonparametric multiplicative regression (NPMR) in HyperNiche™ to quantify the relationship between species' cover and environmental gradients (McCune 2009). Predictors were scores of the three ordination axes. These scores represented an integrated measure of complex environmental gradients associated with dominant patterns of herbaceous community composition. Response variables were the cover of each species using a local mean estimator and Gaussian kernel function. To control for potential interactions between axes, response curves were generated using partial models and focal variables (McCune 2009). A final NPMR model was run using the three axes' scores as predictors. Final model fit was assessed with a cross-validated R^2 (McCune 2009).

Hierarchical agglomerative cluster analysis was used to identify groups of sites differing in community composition (McCune & Grace 2002). Multivariate differences in community composition between identified groups were tested using multiresponse permutation procedures (MRPP) ($\alpha = 0{\cdot}05$). Identified groups were overlaid onto ordinations to accentuate relationships between groups and environmental gradients. Multivariate differences in relativized environmental variables between groups were tested with MRPP. Differences in individual environmental variables between groups were assessed with ANOVA ($\alpha = 0{\cdot}10$), and Bonferroni-adjusted 90% confidence intervals were used to quantify differences between groups.

STRUCTURAL EQUATION MODELLING

In our study, an initial conceptual model was used as a SEM meta-model, representing a family of possible models (Fig. 1, Table 1). Our modelling process considered the available observed variables to identify 'indicator variables' (the observed variables that will serve as proxies for conceptual variables in the meta-SEM) using procedures described in Grace *et al.* (2012). Except for 'Potential Safe Sites', all model constructs were represented using single indicator variables. *Bromus tectorum* cover was selected as the indicator to measure 'Invasion Magnitude'. Bunchgrass and sagebrush cover were selected to measure their abundances. The three NMS ordination axes of bunchgrass species' cover data were used to develop an indicator of 'Bunchgrass Community Composition'. Distance from nearest water was selected as the indicator to measure cumulative 'Cattle Grazing Intensity'. Heat load was selected to measure 'Heat load Exposure', and percent sand content at 0–15 soil depth was selected to measure 'Soil Physical Properties'. The proportion of transects covered by large gaps (>200 cm in length) was selected as the measure of 'Community Gap Structure'. Two indicators were selected to represent 'Potential Safe Sites' – BSC and cover of bare soil.

All SEM analyses were conducted using AMOS 18.0 software (SPSS 2010). Maximum likelihood procedures were used for model evaluation and parameter estimation. Model fit was

evaluated by sequentially evaluating likelihood ratios by using the single-degree-of-freedom chi-squared goodness-of-fit statistic. Modification indices were used to evaluate the need to include links or error correlations not in the original model. This process produced a final inferential model. The stability of the final model was evaluated by introducing other available indicators to determine whether they represented additional contributing information. For example, our initial indicator for cattle grazing intensity was 'distance from nearest water'. The three alternative potential indicators (cow pie frequency, cow pie density and bunchgrass basal area) for this construct did not improve model fit or amount of variation in cheatgrass dominance explained and were no longer included.

Results

PATTERNS OF INVASIBILITY – CONVENTIONAL MULTIVARIATE RESULTS

Nearly 92% of variation in community composition was explained by the final ordination (Fig. 2). Axis 1 was the dominant axis explaining 60·9% of variation in composition data. Axis 1 was a strong gradient of decreasing cattle grazing disturbance and heat stress (Fig. 2): dung density ($r = -0{\cdot}35$); dung frequency ($r = -0{\cdot}36$); distance from water ($r = 0{\cdot}41$); deep-rooted bunchgrass basal area ($r = 0{\cdot}71$); and heat loads ($r = -0{\cdot}44$). In addition, BSC cover, soil aggregate stability and proportion of soil aggregate stability values rated as highly stable increased along Axis 1 (Fig. 2). The size of and connectivity between gaps and amount of bare soil decreased strongly

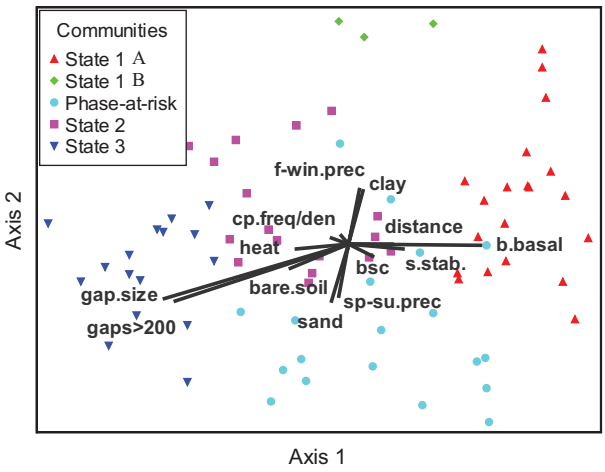


Fig. 2. Ordination of plots in community composition space. Non-metric multidimensional scaling ordination with final stress of 9·92; final instability of <0·01; Monte Carlo test *P*-value < 0·05. Vectors show the strength and direction of correlations between environmental variables and axes. Only variables with significant R^2 (>0·20) are shown. Different plot symbols show groups derived from cluster analysis that differ in composition and environmental factors. State 1A and 1B communities have understoreys dominated by native bunchgrasses; phase-at-risk communities are co-dominated by bunchgrasses and non-natives, and State 2 and State 3 communities are dominated by non-native species.

along Axes 1 and 2 (Fig. 2) (see Table S1, Supporting Information).

Axes 2 and 3 represented weaker relationships explaining 19·3% and 11·6% of the variation, respectively. Axis 2 showed a strong gradient of decreasing sand, increasing clay and increasing fall and winter precipitation (Fig. 2). Axis 3 demonstrated a weaker gradient of decreasing cattle grazing associated with decreasing dung density and frequency and increasing deep-rooted bunchgrass basal area (see Table S1, Supporting Information).

Nonparametric multiplicative regression model sensitivities indicate that Axis 1 was the best predictor of non-native species. The strength of the relationship between cover of native species and these three axes varied considerably (Fig. 3; see Table S2, Supporting Information). *P. spicata*, *A. thurberianum*, *P. secunda* and forbs had strong positive relationships with Axis 1, *P. secunda* and forbs had strong positive relationships with Axis 2, and *Elymus elymoides* had a strong positive relationship with Axis 3 (Fig. 3).

Cluster analysis identified five distinct groups of communities with 0% of the information remaining (MRPP using species data: $A = 0{\cdot}33$, $P < 0{\cdot}01$; Fig. 4; See Tables S3 and S4, Supporting Information). Several species were uniquely associated with one or more groups (Fig. 4; See Table S3, Supporting Information). Combined heat loads, soil physical properties, BSC cover, bare soil cover, soil stability, community gap structure and cattle grazing intensity differed significantly among groups (MRPP using environmental data: $A = 0{\cdot}59$, $P < 0{\cdot}0001$; Fig. 5; See Table S4, Supporting Information).

State 1 consisted of two groups (1A and 1B) of communities with an intact herbaceous understorey dominated by native bunchgrasses and forbs (Fig. 4). Thirty-one percentage of study plots were in one of these groups. State 1 also contained phase-at-risk communities (communities at risk of crossing a biological threshold to being dominated by *B. tectorum*; 25% of study plots) with an understorey co-dominated by native species and *B. tectorum*. States 2 (23% of study plots) and 3 (21% of study plots) consisted of communities that have crossed a biological threshold and had understories dominated by *B. tectorum* and the non-native annual forb, *Lepidium perfoliatum*.

Communities in Groups 1A and 1B had the lowest levels of cattle grazing combined with the smallest and least connected gaps between perennial vegetation (Fig. 5). Group 1B communities had higher heat loads and finer-textured soils compared to those of Group 1A. Communities comprising phase-at-risk communities were characterized by intermediate levels of cattle grazing, heat loads, water stress and size of and connectivity between gaps (Fig. 5).

State 2 communities were characterized by intermediate to high levels of cattle grazing and intermediate levels of heat loads and water stress. State 3 communities had the highest levels of cattle grazing and bare soil cover, largest and most connected gaps and lowest soil aggregate stability (Fig. 5).

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society, *Journal of Applied Ecology*

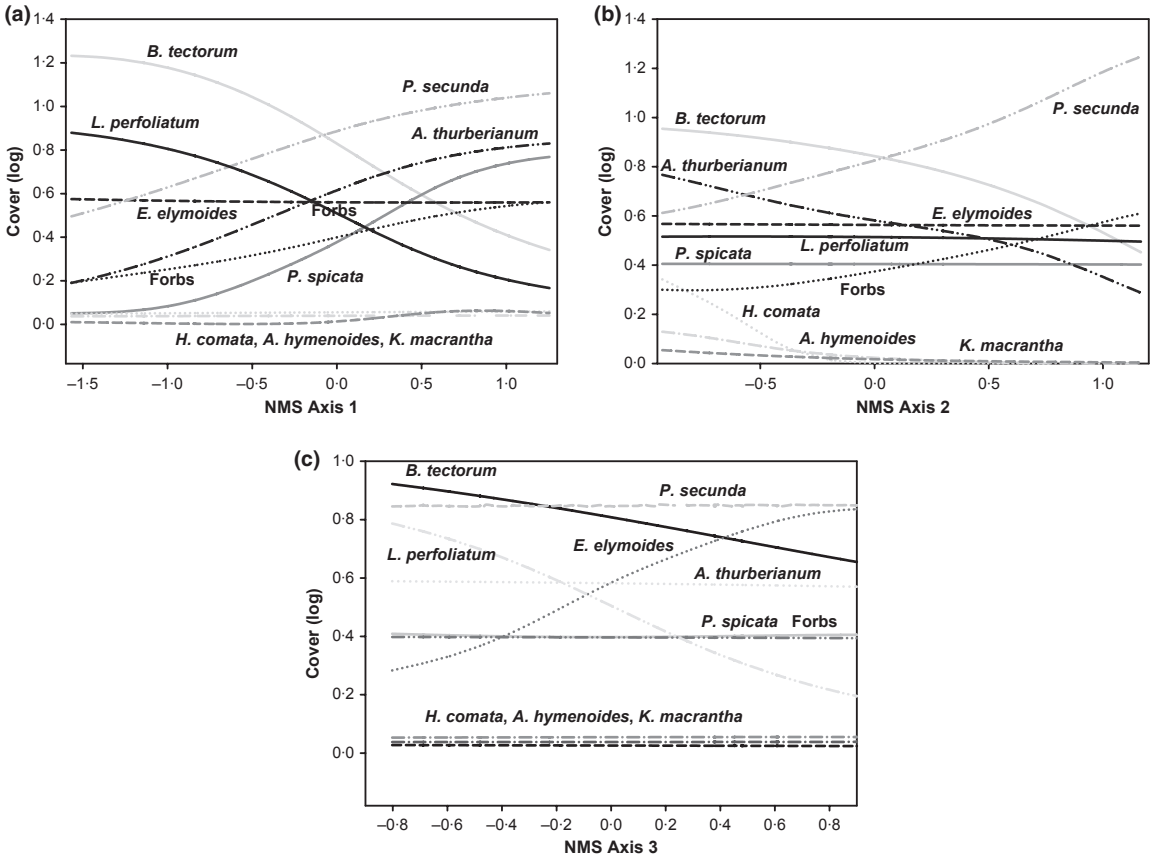


Fig. 3. Nonparametric multiplicative regression response curves showing relationship between species cover and gradients represented by non-metric multidimensional scaling ordination axes. Axis 1 is a gradient of decreasing cattle grazing intensity and heat load exposure (a), Axis 2 is a gradient of decreasing water stress (b), and Axis 3 is a gradient of decreasing cattle intensity (c).

STRUCTURAL EQUATION MODELLING RESULTS

The final SEM model ($\chi^2 = 18{\cdot}88$; $P = 0{\cdot}54$; 20 d.f.) showed very close fit between model and data. A number of the initially hypothesized relationships (Table 1) were not supported by data. Sagebrush abundance did not help explain invasion magnitude, either directly or indirectly. As a result, that variable was removed from the final model. Heat load exposure, cattle grazing intensity and native bunchgrass cover were indirect predictors of invasion magnitude in the final model (Fig. 6). Unanticipated in the initial model was dependence of safe sites on heat loads and sand, and dependence of bunchgrass composition on sand content. The final model explained 72% of the variation in the magnitude of invasions among sites.

Concerning strengths of linkages in the final model, changes in community gap structure, that is, increases in the size of and connectivity between gaps among native plants, were predictive of higher levels of *B. tectorum* cover ($r = 0{\cdot}83$). Native bunchgrass cover and composition were not direct predictors of *B. tectorum* cover, rather they were indirect predictors through their relationship to gaps. Gaps characterized by bare soil had a strong positive association with *B. tectorum* cover ($r = 0{\cdot}38$), whereas gaps characterized by BSC cover had a strong negative association with *B. tectorum* cover ($r = -0{\cdot}26$).

Cattle grazing intensity was positively associated with *B. tectorum* cover through three independent pathways. Because distance from water is inversely related to cattle grazing levels, positive path coefficients indicate a negative relationship between cattle grazing and the response variable in the model (Fig. 6). Thus, model results imply that pathways from cattle grazing to *B. tectorum* cover propagate through (i) negative influences on bunchgrass abundance (0·34), (ii) negative influences on BSC abundance (0·29) and (iii) impacts on bunchgrass community composition (Axis 2) (0·22). There was no evidence that cattle grazing directly decreased or increased *B. tectorum* cover independent of these stated routes.

High levels of heat load exposure were associated with lower levels of bunchgrass (−0·46) and BSC (−0·36) abundance. Coarser-textured soils were more likely to have higher levels of *B. tectorum*, regardless of the other factors (i.e. a direct linkage of 0·48). Coarser-textured soils also had an indirect path through effects on bare soil cover and bunchgrass community composition (Axis 3) that increased *B. tectorum* cover.

By adding up the path strengths, it is possible to compute what is referred to as 'total effects' of predictors on

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society,

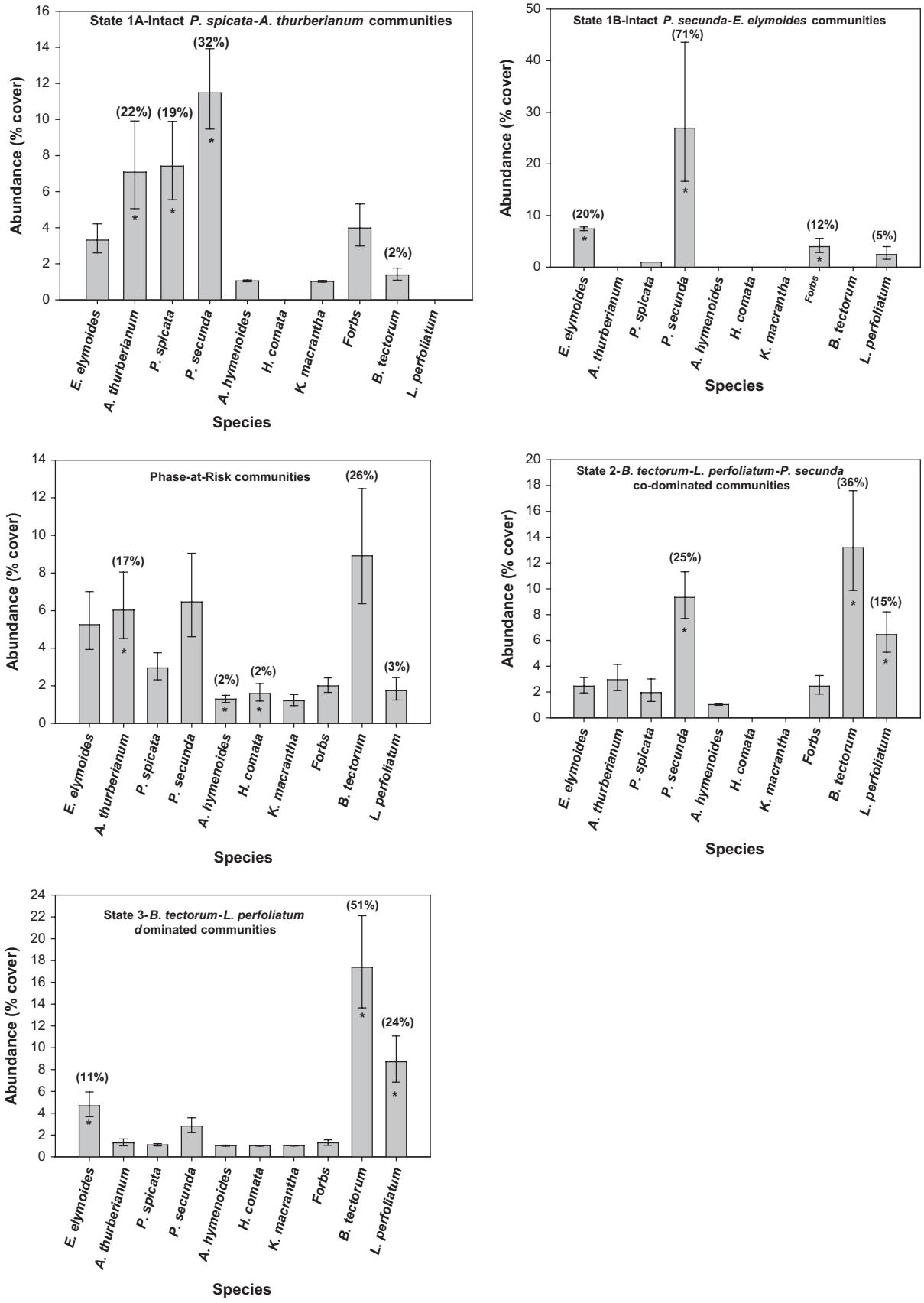


Fig. 4. Community composition of five groups derived from cluster analysis. *Denotes species with highest three indicator values for the group from indicator species analysis. Reported values are back-transformed means, and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of total cover of the group.

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society, *Journal of Applied Ecology*

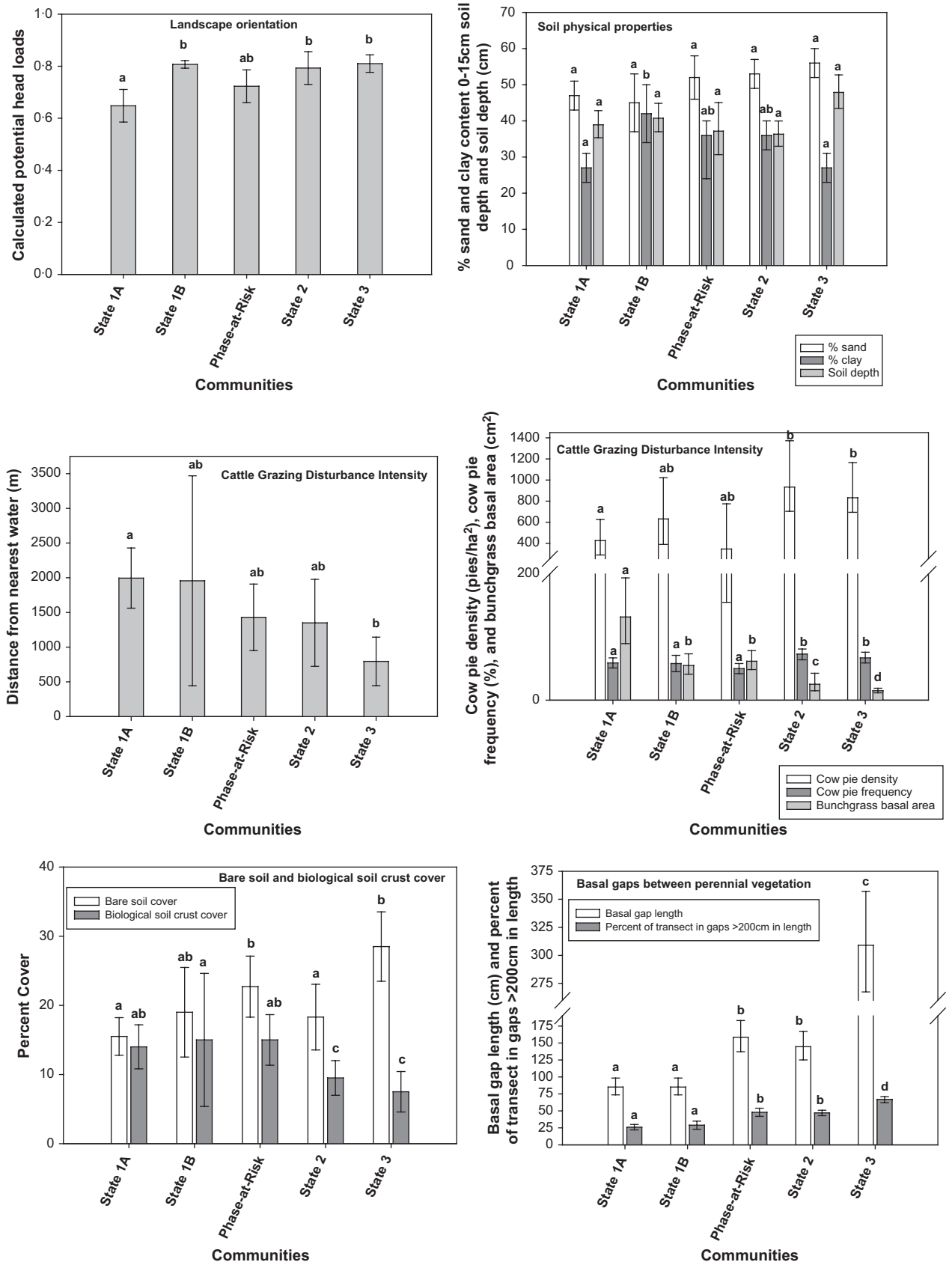


Fig. 5. Differences in heat loads, soil physical properties, biological soil crusts, bare soil cover, soil stability, community gap structure and cattle grazing intensity of five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower-case letters above bars indicate significant differences between groups ($\alpha = 0{\cdot}10$).

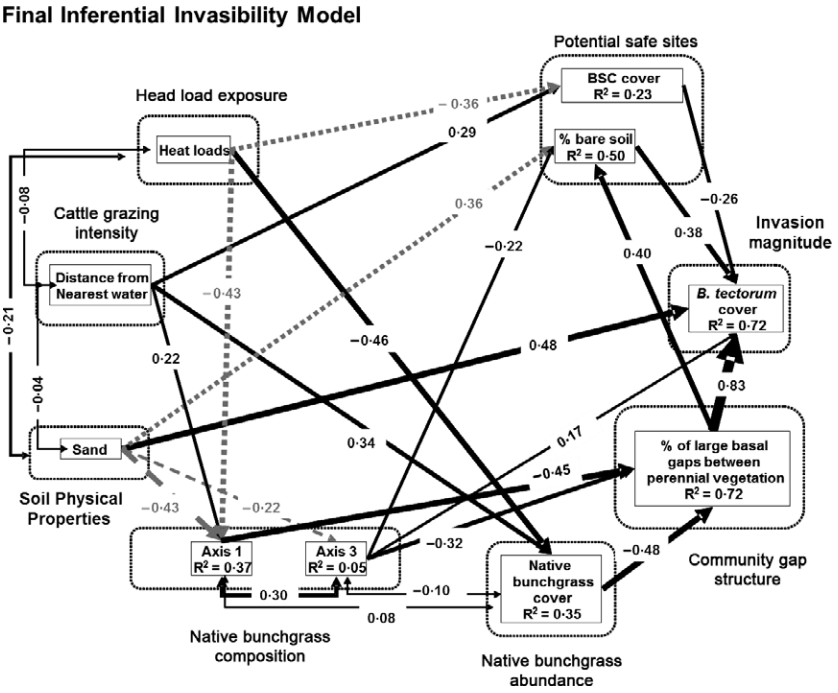


Fig. 6. Final inferential model of *Artemisia* ecosystem invasibility. Single-headed arrows represent significant linkages ($\alpha = 0{\cdot}05$). Double-headed arrows indicate significant correlations between variables and their residuals. The magnitudes of standardized path coefficients are represented by line thicknesses. Dotted grey lines are unanticipated significant paths. Because distance from water is inversely related to cattle grazing intensity (i.e. grazing intensity increases with decreasing distance), positive path coefficients and correlations between grazing intensity and variables indicate an inverse relationship (i.e. increasing cattle grazing intensity decreases bunchgrass abundance). R^2 values depict the proportion of variation of endogenous variables explained by the model. The dotted boxes depict conceptual variables of the meta-structural equation modelling (Fig. 1).

downstream responses. Computed total effects of predictor variables on *B. tectorum* in order of importance were as follows: (i) community gap structure (0·68), (ii) soil physical properties (0·42), (iii) safe sites (bare soil cover, 0·38), (iv) heat load exposure (0·37), bunchgrass community composition (NMS#1, −0·31), (v) safe sites (BSC cover, −0·26), (vi) cattle grazing disturbance (−0·26), (vii) bunchgrass abundance (−0·24) and (viii) bunchgrass community composition (NMS#3, 0·04).

Discussion

By combining SEM with an observational approach, we were able to gain important new insight into the relative importance of the numerous factors determining the magnitude of *B. tectorum* invasions of *Artemisia* ecosystems and gain valuable insight into potential underlying mechanisms. Our results provide strong support for some *a priori* hypothesized mechanisms (i.e. cattle trampling reduces bunchgrass and BSC abundance) and no support for others (i.e. cattle reduce invasions by grazing *B. tectorum*). Our SEM findings should help prioritize future experiments to test our inferences regarding underlying mechanisms and more landscape-scale observational studies to further evaluate and refine the model and construct predictive models (Grace 2006).

In this study, model results support the idea that a complex causal network of simultaneously operating factors and mechanisms are driving invasion of *B. tectorum* in *Artemisia* ecosystems. Based upon the SEM results, shifts in community structure, as measured by the size of and connectivity of gaps between native plants, exert a strong positive effect on the magnitude of *B. tectorum* invasion. This finding is consistent with growing evidence in semi-arid and arid ecosystems showing that increases in gap connectivity (Busso & Bonvissuto 2009; Okin *et al.* 2009) and changes in how species abundance is distributed in a community (James *et al.* 2008) are associated with a loss of ecosystem resistance to invasion (Scheffer *et al.* 2009). We define resistance as the collective ability of the resident sagebrush community to limit *B. tectorum* dominance in the face of invasion (Chambers *et al.* 2007). Increases in the connectivity of these gaps were associated with a dramatic increase in the magnitude of such invasions (Okin *et al.* 2009). This loss of resistance to invasion probably increases the magnitude of *B. tectorum* dominance after subsequent disturbances and may set the stage for a regime shift to *B. tectorum*-dominated grasslands with the next fire (Scheffer *et al.* 2009).

Our research suggests that two environmental factors influence the inherent resistance of *Artemisia* ecosystems to *B. tectorum* invasion. Communities located on coarser-textured soils or characterized by higher potential heat loads (Stewart & Hull 1949) were inherently least resistant to *B. tectorum* invasion. These communities are characterized by higher levels of water stress and lower productivity. The inherent structure of these communities that consists of larger and more connected gaps among perennial vegetation and higher amounts of bare soil may make them vulnerable to other disturbances that increase the size of gaps.

Consistent with other studies, biotic resistance from resident bunchgrass and BSC communities played pivotal roles and appears to limit the magnitude of *B. tectorum* invasion (Richardson & Pysek 2006). Water availability is the primary controlling factor of seedling establishment in these ecosystems (Schupp 1995). Several studies have found a strong negative association between BSC community integrity and *B. tectorum* abundance (Ponzetti, McCune & Pyke

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society, *Journal of Applied Ecology*

2007; Ponzetti & McCune 2008) and showed that BSCs reduce *B. tectorum* germination and establishment rates by impeding root penetration and growth (Serpe *et al.* 2008). Our findings suggest that BSC communities are especially important in limiting the magnitude of *B. tectorum* invasions in gaps between perennial vegetation by minimizing potential safe sites for establishment.

Consistent with other studies, we found that bunchgrasses reduced the magnitude of *B. tectorum* invasions most likely by reducing water and nutrient availability (Chambers *et al.* 2007; Prevéy *et al.* 2010). Our findings provide important insight into this mechanism. Nearly all the biotic resistance effect was indirect through a strong direct effect of bunchgrass abundance and composition on community structure. By limiting the size and connectivity of gaps, bunchgrasses likely minimize resources available to *B. tectorum* spatially. Further, three species, *P. spicata*, *A. thurberianum* and *P. secunda,* appear to be especially important determinants of such resistance. *P. spicata* and *A. thurberianum* are dominant deep-rooted bunchgrasses with most active growth in later spring, whereas *P. secunda* is a shallow-rooted bunchgrass that is active in late winter and early spring. This combination of differing structure and phenology reflects their differing abilities to acquire resources at different soil depths (James *et al.* 2008) and seasons and thereby provide continuous interaction with *B. tectorum* and collectively limit available resources temporally and at different soil depths.

By controlling for several potentially confounding factors (Knick *et al.* 2011), we gained important insights into the role of cattle grazing as a determinant of ecosystem resistance to *B. tectorum* invasion. We found no evidence that cattle grazing, even at the high intensities 100 m from the nearest water development, reduced *B. tectorum* cover. To the contrary, we found strong evidence that increasing cattle grazing intensity indirectly promotes an increase in the magnitude of *B. tectorum* dominance. Cattle herbivory was found to be associated with reduced native bunchgrass abundance, shifts in bunchgrass composition to only the most grazing-tolerant species and aggregated bunchgrasses beneath protective sagebrush canopies (Reisner 2010). These collective cattle-induced changes thus appear to ripple through the community by increasing the size and connectivity of gaps between perennial vegetation. As gaps get bigger and more connected, both live and dead (litter) herbaceous soil cover decreases and the amount of bare soil increases. Cattle trampling reduced resistance within these larger gaps by reducing BSC cover.

Changes in community structure and how species' abundance is distributed in the community may increase general resource availability (James *et al.* 2008). As cattle grazing increased, *P. spicata*, *A. thurberianum* and *P. secunda* cover decreased, *E. elymoides* cover did not change, and *B. tectorum* cover increased. These shifts parallel the relative differences in grazing avoidance and tolerance mechanisms among these species. Cattle grazing introduced a novel disturbance regime into this system where most bunchgrasses are highly sensitive to herbivory (Mack & Thompson 1982). To the contrary, *B. tectorum* exhibits a collection of grazing avoidance and tolerance attributes that makes it extremely tolerant of even highly intensive grazing (Vallentine & Stevens 1994; Hempy-Mayer & Pyke 2009). Because of its attributes (Chambers *et al.* 2007), *B. tectorum* is well positioned to take maximum advantage of this window of invasion opportunity by exploiting larger and more connected gaps.

If the goal is to conserve and restore resistance of these systems to invasion, managers should consider focusing their efforts on maximizing the pre-emption of resources provided by BSC and bunchgrasses. We suggest three priorities: first, maintain and/or restore high overall bunchgrass cover and community structure characterized by spatially dispersed bunchgrasses in interspaces and small gaps between such individuals to maximize the capture of resources; second, maintain and/or restore a diverse assemblage of bunchgrass species with different spatial and temporal patterns of resource use to maximize capture of resources at different soil depths and times; third, maintain and/or restore a BSC community to limit safe sites for *B. tectorum* establishment within gaps.

Our findings suggest that multiple factors (bunchgrass cover, BSC cover, cattle grazing, etc.) may influence the susceptibility of these ecosystems to *B. tectorum* invasion. Importantly, many of these influences are mediated by the size and connectivity of gaps, as well as the conditions of gaps. Thus, gaps in perennial vegetation may serve as an important early warning indicator of when cattle grazing or other stressors are compromising resistance of these systems to *B. tectorum* invasion. Our findings raise serious concerns regarding proposals to use cattle grazing to control *B. tectorum* in these systems where remnant bunchgrass communities persist (Vallentine & Stevens 1994). In contrast, our findings support recent guidance for passively restoring resistance of these systems by reducing grazing levels (Pyke 2011). Future research should focus on gathering information concerning the size of and connectively of such gaps across a range of ES consistent with maintaining resistance. These data could be used to develop indicators for adaptive management frameworks to conserve and restore these endangered systems.

Acknowledgements

We thank our field assistants and families. This is contribution #71 from the Sagebrush Steppe Treatment and Evaluation Project, funded by the US Joint Fire Sciences Program and by the US Geological Survey Forest and Rangeland Ecosystem Science Center and Oregon State University. The use of any trade, product or firm name is for descriptive purposes only and does not imply endorsement by the US Government.

References

Agrawal, A.A., Ackerly, D.A., Adler, F., Arnold, B., Cáceres, C., Doak, D.F., Post, E., Hudson, P., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J.J., Strauss, S.Y., Turner, M.G. & Werner,

E. (2007) Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment*, **5**, 145–152.
Beever, E.A., Huso, M. & Pyke, D.A. (2006) Multi-scale responses of soil stability and invasive plants to removal of non-native grazers from an arid conservation reserve. *Diversity and Distributions*, **12**, 258–268.
Briske, D.D. & Richards, J.H. (1995) Plant responses to defoliation: a physiological, morphological, and demographic evaluation, pp. 625–710. *Wildland Plants: Physiological Ecology and Development Morphology* (eds D.J. Bedunah & R.E. Sosebee), pp. 710. Society for Range Management, Denver, CO.
Busso, C. & Bonvissuto, G. (2009) Structure of vegetation patches in northwestern Patagonia, Argentina. *Biodiversity and Conservation*, **18**, 3017–3041.
Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E. & Whittaker, A. (2007) What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, **77**, 117–145.
Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J. & Pasteris, P.P. (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the United States. *International Journal of Climatology*, **27**, 935–969.
Davies, K.W., Bates, J.D. & Miller, R.F. (2007) Environmental and vegetation relationships of *Artemisia tridentata* ssp. *wyomingensis* alliance. *Journal of Arid Environments*, **70**, 478–494.
Davis, M.A., Grime, J.P. & Thompson, J.N. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
Fowler, N.L. (1988) What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology*, **69**, 947–961.
Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific interaction competition in natural communities: a review of field experiments with plants. *The American Naturalist*, **139**, 771–801.
Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.
Grace, J.B., Youngblood, A. & Scheiner, S.M. (2009) Structural equation modeling and ecological experiments. *Real World Ecology: Large-Scale and Long-Term Case Studies and Methods*, Chapter 2 (S. Miao, S. Carstenn & M. Nungesser), pp. 19–45. Springer Verlag, New York.
Grace, J.B., Schoolmaster Jr, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M. & Schweiger, E.W. (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**, article 73.
Griffith, A.B. (2010) Positive effects of native shrubs on *Bromus tectorum* demography. *Ecology*, **91**, 141–154.
Grime, J.P. (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1182.
Hempy-Mayer, K. & Pyke, D.A. (2009) Defoliation effects on *Bromus tectorum* seed production: implications for grazing. *Rangeland Ecology & Management*, **61**, 116–123.
Herrick, J.E., Van Zoo, J.W., Havstad, K.M., Burkett, L.M. & Whitford, W.G. (2005) *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems*, Vol 1. US Department of Agriculture, Agriculture Research Station, Jornada Experimental Range, Las Cruses, NM, pp. 42.
James, J., Davies, K., Sheley, R. & Aanderud, Z. (2008) Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. *Oecologia*, **156**, 637–648.
Knick, S.T., Hanser, S.E., Miller, R.F., Pyke, D.A., Wisdom, M.J., Finn, S.P., Rinkes, E.T. & Henny, C.J. (2011) Ecological influence and pathways of land use in sagebrush. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 203–251. University of California Press, Berkeley, CA.
Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of exotic plant invasions. *Ecology Letters*, **7**, 975–989.
Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
Mack, R.N. & Thompson, J.N. (1982) Evolution in steppe with few large, hooved mammals. *The American Naturalist*, **119**, 757–773.
McCune, B. (2007) Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. *Journal of Vegetation Science*, **18**, 751–754.
McCune, B. (2009) *Nonparametric Multiplicative Regression for Habitat Modeling*. Oregon State University, Corvallis, OR.
McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach, OR.
Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J. & Hild, A.L. (2011) Characteristics of sagebrush habitats and limitations to long-term conservation. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 145–184. University of California Press, Berkeley, CA.
Okin, G.S., Parsons, A.J., Wainwright, J., Herrick, J.E., Bestelmeyer, B.T., Peters, D.C. & Fredrickson, E.L. (2009) Do changes in connectivity explain desertification? *BioScience*, **59**, 237–244.
Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.
Ponzetti, J.M. & McCune, B.P. (2008) Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *The Bryologist*, **104**, 212–225.
Ponzetti, J.M., McCune, B. & Pyke, D.A. (2007) Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. *The Bryologist*, **110**, 706–722.
Prevéy, J., Germino, M., Huntly, N. & Inouye, R. (2010) Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology*, **207**, 39–51.
Pyke, D.A. (2011) Restoring and rehabilitating sagebrush habitats. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 531–548. University of California Press, Berkeley, CA.
Reichenberger, G. & Pyke, D.A. (1990) Impact of early root competition on fitness components of four semiarid species. *Oecologia*, **85**, 159–166.
Reisner, M.D. (2010) *Drivers of plant community dynamics in sagebrush steppe ecosystems: cattle grazing, heat and water stress*. Dissertation, Oregon State University, Corvallis, OR, pp. 286.
Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.
Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M. & Sugihara, G. (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53–59.
Schiffman, P.M. (1997) Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. *Assessment and Management of Plant Invasions* (eds J.O. Luken & J.W. Thieret), pp. 87–94. Springer-Verlag, New York, NY.
Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.
Serpe, M., Zimmerman, S., Deines, L. & Rosentreter, R. (2008) Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil*, **303**, 191–205.
SPSS (2010) *Amos 18.0*. SPSS, Chicago, IL.
Stewart, G. & Hull, A.C. (1949) Cheatgrass (*Bromus Tectorum* L.): an ecologic intruder in southern Idaho. *Ecology*, **30**, 58–74.
Vallentine, J.F. & Stevens, A.R. (1994) Use of livestock to control cheatgrass-a review. *Proceedings of Symposium on Ecology, Management, and Restoration of Intermountain Rangelands*, Boise, ID, May 18–22, 1992, pp. 202–206.

Received 28 November 2012; accepted 27 March 2013
Handling Editor: Andy Sheppard

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Relationships between environmental variables and ordination axes.

Table S2. Relationships between species abundance and ordination axes.

Table S3. Indicator species analysis of groups.

Table S4. Pairwise MRPP comparisons of groups.

© 2013 The Authors. Journal of Applied Ecology © 2013 British Ecological Society, *Journal of Applied Ecology*

Ecological Applications, 0(0), 2019, e02016
© 2019 by the Ecological Society of America

Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities

Heather T. Root [1,4] Jesse E. D. Miller,[2] and Roger Rosentreter[3]

[1]*Botany Department, Weber State University, Ogden, Utah 84401 USA*
[2]*Department of Biology, Stanford University, Stanford, California 94304 USA*
[3]*Biology Department, Boise State University, Boise, Idaho 83725 USA*

Citation: Root, H. T., J. E. D. Miller, and R. Rosentreter. 2019. Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities. Ecological Applications 00(00):e02016. 10.1002/eap.2016

Abstract. Exotic invasive plants threaten ecosystem integrity, and their success depends on a combination of abiotic factors, disturbances, and interactions with existing communities. In dryland ecosystems, soil biocrusts (communities of lichens, bryophytes, and microorganisms) can limit favorable microsites needed for invasive species establishment, but the relative importance of biocrusts for landscape-scale invasion patterns remains poorly understood. We examine effects of livestock grazing in habitats at high risk for invasion to test the hypothesis that disturbance indirectly favors exotic annual grasses by reducing biocrust cover. We present some of the first evidence that biocrusts increase site resistance to invasion at a landscape scale and mediate the effects of disturbance. Biocrust species richness, which is reduced by livestock grazing, also appears to promote native perennial grasses. Short mosses, as a functional group, appear to be particularly valuable for preventing invasion by exotic annual grasses. Our study suggests that maintaining biocrust communities with high cover, species richness, and cover of short mosses can increase resistance to invasion. These results highlight the potential of soil surface communities to mediate invasion dynamics and suggest promising avenues for restoration in dryland ecosystems.

Key words: biocrust; cheatgrass; disturbance ecology; diversity–ecosystem-function relationship; exotic annual grasses; livestock grazing; plant establishment; rangeland; resistance to invasion.

Introduction

Invasion by exotic plants threatens biodiversity (Heywood 1989) and can substantially affect ecosystem services and processes (Vitousek et al. 1996, Williamson 1999, Pimentel et al. 2000). However, drivers of invasion are difficult to generalize and likely include complex interactions among climate, disturbance regimes, traits of native plant communities, and dispersal pressure from potential invaders (Lonsdale 1999). When there is an increase in unused resources, plant communities are expected to be more susceptible to invasion (the fluctuating resource hypothesis; Davis et al. 2000). Because disturbance often results in reduction or loss of native plant communities, it can increase available resources and reduce competitive resistance to potential invaders (Chambers et al. 2007). Access to favorable microsites for establishment, such as sites without native competitors, may be a critical determinant of competitive success (Boeken 2018). Although numerous studies have examined how invasion is affected by characteristics of above-ground plants (Anderson and Inouye 2001, Chambers et al. 2014) and soil microbes (Levine et al. 2006), communities of organisms at the soil surface that modify establishment microsites may be a cryptic driver of invasion dynamics, particularly following disturbance.

Exotic annual grasses have had major impacts on ecosystem services in arid and semiarid ecosystems globally (D'Antonio and Vitousek 1992, Balch et al. 2013). In particular, these invasions are problematic because they degrade habitat quality for native plants and animals (Connelly et al. 2000, Condon and Pyke 2018) and increase wildfire frequency and size (Balch et al. 2013). Exotic annual grasses have occurred in western North America for over a century and have long been associated with intensive livestock grazing and wildfires (Stewart and Hull 1949). Many factors influence the resistance and resilience of sites to exotic annual grass invasion, including climate, soils, topography, established plant communities, and disturbance history (Chambers et al. 2014). Invasion by exotic annual grasses is strongly mediated by the native plant community (Anderson and Inouye 2001, Chambers et al. 2014) and some observational studies have suggested that invasion may be mediated by soil biocrusts (Peterson 2013, Reisner et al. 2013), diverse ground-dwelling communities of lichens, mosses, and free-living algae and bacteria.

Manuscript received 18 June 2019; revised 12 August 2019; accepted 11 September 2019. Corresponding Editor: Deborah A. Neher.
[4] E-mail: heatherroot@weber.edu

Biocrust cover is known to be generally inversely related to exotic annual grass cover, but the mechanisms linking biocrusts to exotic grasses remains incompletely understood. A negative relationship between exotic annual grasses and biocrusts may be caused by litter from the grasses suppressing biocrust development (Dettweiler-Robinson et al. 2013) or by biocrusts reducing germination and establishment of exotic annual grasses (Deines et al. 2007, Slate et al. 2018). Disentangling the relative importance of these processes remains an open question for both basic invasion ecology and applied range management questions. If biocrusts are inhibited by annual grass litter, intervention to reestablish biocrusts could improve resilience after invasion. If biocrusts increase site resistance and prevent invasion, however, a focus on maintaining the integrity of these communities could have long-term ecosystem benefits. Though field studies have suggested that disturbances can reduce biocrusts (Ponzetti and McCune 2001, Peterson 2013), and that biocrusts are negatively associated with exotic annual grasses (Peterson 2013, Reisner et al. 2013), the indirect causal pathway linking disturbance to invasion by exotic annual grasses via biocrusts has not been tested in a broad landscape-level field study.

The arid and semiarid ecosystems that cover approximately one-third of global terrestrial habitats (Schlesinger et al. 1990) typically support sparse vegetation with biocrusts occupying much of the open space between vascular plants (Belnap et al. 2016). Biocrust communities serve many ecosystem functions, such as decreasing erosion (Belnap and Büdel 2016) and contributing to nutrient cycling (Housman et al. 2006). Biocrust communities vary geographically in composition, often containing greater diversity than local vascular plant communities, and biocrusts have high landscape-scale species turnover that likely corresponds to functional trait variation (Root and McCune 2012, Rosentreter et al. 2016, Root et al. 2017). In general, biocrust communities are sensitive to disturbances by livestock grazing and wildfire (Ponzetti and McCune 2001, Ponzetti et al. 2007, Williams et al. 2008, Liu et al. 2009, Root et al. 2017). Following these disturbances, there is typically more bare soil (Reisner et al. 2013, Root et al. 2017), which could provide microsites for plant establishment. Though some studies have linked biocrust diversity with ecosystem functions (Bowker et al. 2010), the effects of different biocrust communities on resistance to invasion by exotic annual grasses are poorly known (Condon and Pyke 2018).

Biocrust communities may provide a critical physical barrier that modifies exotic seed establishment microsites (Serpe et al. 2008), despite being often overlooked because of their cryptic nature. Establishment microsites are central in determining outcomes of competition among plants, particularly for annual grasses in semiarid ecosystems (Boeken 2018, Condon and Pyke 2018). Intact biocrusts may play critical roles in restricting the establishment of exotic annual grasses, which often become dominant because of their speed and success in this early establishment stage (Stewart and Hull 1949). However, experimental studies examining the effects of biocrusts on seedling establishment have shown that biocrusts can either enhance or inhibit seedling establishment (Deines et al. 2007, Pando-Moreno et al. 2014, Slate et al. 2018). It is likely that the outcome of interactions between biocrust communities and establishment of plant seedlings depend on specific functional traits of each, such as continuity and thickness of the crust community as well as seed size and shape (Serpe et al. 2006, Slate et al. 2018). To effectively restore biocrust communities that maintain desirable ecosystem functions, an understanding of which functional groups are most effective at increasing site resistance is needed.

The exotic annual grass cheatgrass (*Bromus tectorum*) has high enough abundance to influence wildfire behavior (>15% cover) across 31% of the Intermountain West in North America (Bradley et al. 2018), and in this region over 40% of the native sagebrush (*Artemisia*) habitats are predicted to be at risk of displacement by cheatgrass in the next decades (Suring et al. 2005). Invasion by cheatgrass varies across the western United States with climate, elevation, and soil characteristics (Pechanec et al. 1937, Chambers et al. 2014). Habitats most susceptible to invasion include salt desert (dominated by species of *Atriplex*) and Wyoming big sagebrush (dominated by *Artemisia tridentata* ssp. *Wyomingensis*) such as those found in the Snake River Plain in southwestern Idaho (Chambers et al. 2014). We focus on these susceptible habitats to examine the effects of livestock grazing disturbance on biocrusts and exotic annual grasses. We capitalized on the presence of a military reservation with access restrictions to characterize undisturbed biocrust communities in a region that is otherwise widely disturbed. We focused on two main objectives: (1) test whether livestock grazing promotes exotic annual grasses directly or indirectly via effects on biocrust lichens and bryophytes and (2) explore whether biocrust lichen and bryophyte functional groups or species vary in how they respond to grazing disturbance or restrict exotic annual grasses.

Methods

Field sampling

We sampled 26 plots within and adjacent to the Idaho Army National Guard Orchard Combat Training Center south of Boise, Idaho on the Snake River Plain (Fig. 1) between 2014 and 2017. This steppe habitat is characterized by hot, dry summers and cold, moist winters with annual precipitation averaging 20–25 cm and elevation from 671 to 975 m. Soils are derived from volcanic ash and basalts. Disturbances include historic and current livestock grazing, roads, military training and recreational trails. In this study, we augmented previous sampling that had focused on biodiversity and community composition in five native-dominated habitats (described

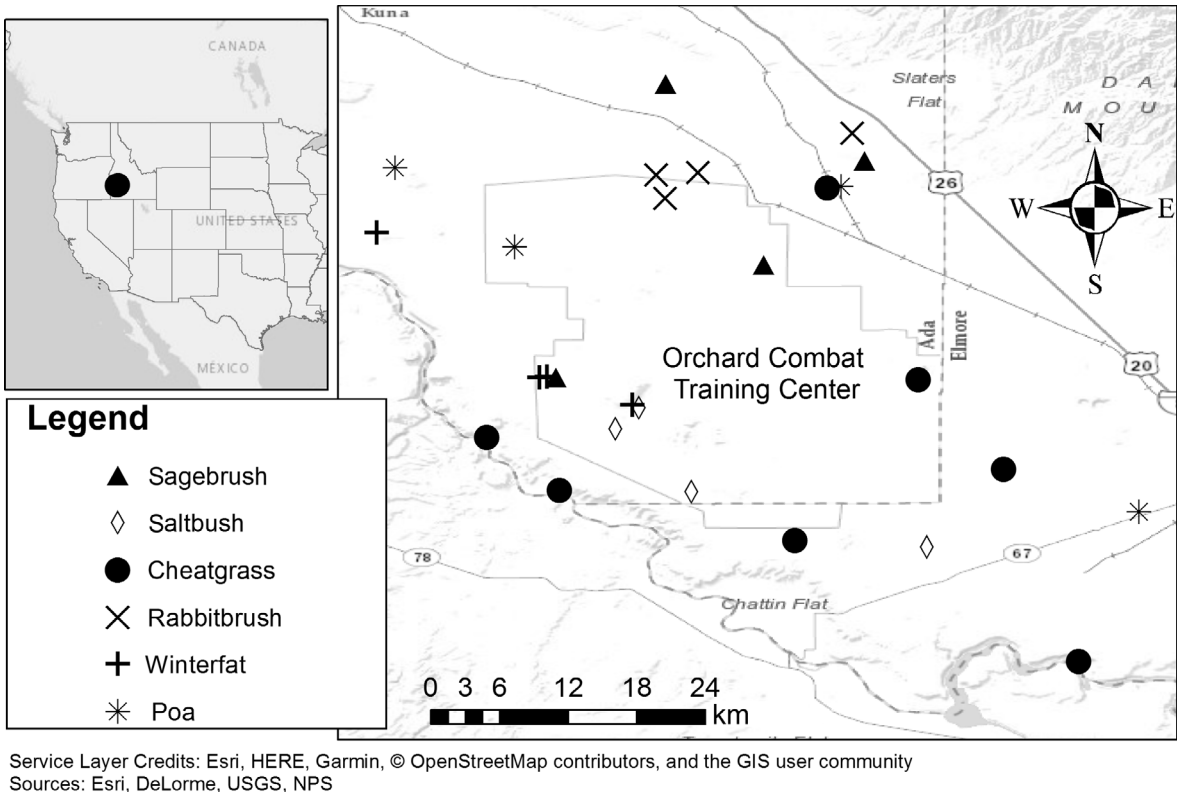


FIG. 1. Map of 26 plots in our study area in southwestern Idaho, USA symbolized by habitat type (these plant communities are described thoroughly in Rosentreter and Root [2019]).

in Rosentreter and Root 2019) with seven additional sites dominated by cheatgrass (*Bromus tectorum*). These sites were randomly selected with stratification to include a fairly even number of plots across grazing intensities and vegetation types. Low grazing intensity plots were randomly chosen within either protected exclosures or near perimeter fences that partially limit livestock movement. Selection criteria included: no roads through plots, no salt blocks or livestock watering troughs within 1/4 mile of plots (1 mile = 1.6 km), and no plow and seeded sites within plots.

To sample biocrust communities and vegetation, we used a modified version of the Forest Health Monitoring study plot protocol (McCune et al. 1997), with 30 min to 2 h examining each 34.7 m radius (0.4 ha) plot (McCune et al. 2009, Root and McCune 2012, Rosentreter and Root 2019). We assigned biocrust species abundance based on number of individuals or colonies: 0 (absent), 1 (≤5), 2 (5–10), and 3 (>10). We also recorded total percent cover of biocrust lichens and bryophytes, and vascular plant cover by species.

We collected samples of each biocrust lichen and bryophyte within the plot. We curated, identified, and assigned functional groups using standard methods (Brodo et al. 2001, McCune and Rosentreter 2007). A full list of biocrust species and their associated functional groups was reported in Rosentreter and Root (2019). Voucher specimens were deposited into the Snake River Plain herbarium at Boise State University (SRP) or with the Idaho Army National Guard. We combined vascular plants into functional groups using the USDA Plants Database (*available online*).[5] Exotic annual grasses were comprised mostly of *Bromus tectorum*, but also included *Eremopyrum triticeum* and *Taeniatherum caput-medusae*. Perennial grasses included several native species with *Poa secunda* being the most abundant. It also included the *Agropyron cristatum* complex, which is not native; however, this plant only occurred in trace amounts at two plots.

We scored grazing levels in each plot using three categories modified from Root and McCune (2012): Low grazing intensity plots had no fresh dung or heavily grazed plants. Medium intensity plots had only one or two fresh dung piles in the plot or some plants that had been partially eaten by livestock. High grazing intensity plots contained at least three fresh dung piles and abundant evidence of grazing on shrubs, forbs or grasses. In assessing evidence of grazing on vegetation, we evaluated whether there was evidence that plants had been eaten (for example, grass bases with grazed tops), but we did not use plant community composition to evaluate grazing intensity. Our data set included nine plots with

[5] https://plants.usda.gov

low, eight with medium, and nine with high intensity grazing.

Analysis

We used an analysis of variance (ANOVA) in the software R (v. 3.5.2; R Development Core Team 2018) to determine whether biocrust cover or richness was related to livestock grazing intensity. We performed pairwise comparisons using a Tukey correction for multiple tests. We used the same approach to determine whether exotic annual grasses or perennial grasses were related to livestock grazing intensity. Prior to analysis, we log-transformed exotic annual grass cover to better meet model assumptions.

To explore these direct and indirect relationships among grazing intensity, biocrust cover, and exotic annual grass cover, we used structural equation modeling (SEM). SEM is an analytic framework that models hypothesized networks of causation, making it ideal for analyzing the relative strength of direct and indirect relationships (Grace 2006, Miller et al. 2015). Multicollinearity among predictors can cause challenges in SEM because it can be difficult to isolate the effects of strongly correlated variables and their inclusion can inflate variance estimates (Grace 2006). To evaluate whether this was likely to be a problem in our data sets, we examined the correlation matrix among all variables (Appendix S1: Tables S1, S2). We then created a priori SEM meta-models with hypothesized pathways of causation (Appendix S1: Fig. S1, Table S3), including both direct effects of grazing on exotic annual grass cover, as well as indirect effects mediated by biocrust variables. After modeling all hypothesized paths, we reran the model excluding paths that were nonsignificant, following Grace's (2006) recommended process for refining SEMs. We evaluated model fit with the χ^2 statistic, for which high P values indicate adequate fit and low P values suggest lack of fit. We further evaluated fit using the directed separation (d-sep) statistic for each model, which is more conservative with smaller sample sizes, and is interpreted similarly to the χ^2 statistic (Shipley 2009). Prior to modeling, we examined histograms and scatterplots to visualize variable distributions, then log-transformed exotic annual grass and perennial grass cover to better meet model assumptions. Although grazing intensity was ordinal, we treated it as continuous following Grace's (2006) recommendation, and this choice seems to be supported by the approximately linear increase of biocrust richness with decreasing grazing intensity (see *Results*). All variables were z-scaled prior to analysis (Grace 2006), and SEMs were analyzed using the software R (v. 3.5.2 R Development Core Team 2018) in the package *piecewiseSEM* (v. 2.0.2; Lefcheck 2016). A potential path that was not in our a priori model could suggest that exotic annual grasses affect biocrust cover (marked by # in Fig. 2A and Appendix S1: Fig. S1). Such recursive paths cannot be specified in *piecewiseSEM*, so we evaluated the final model (Fig. 2A) in the package *lavaan* (v. 0.6-3; Rosseel 2012) with this recursive path. This allowed a post hoc test of whether the relationship between exotic annual grasses and biocrust cover was indeed better supported in the opposite direction than we had conceived it.

We used a second SEM to explore the effects of particular biocrust functional groups on total biocrust cover and exotic annual grass cover. We represented biocrust functional group abundance using relativized cover to minimize multicollinearity issues. This was calculated by summing abundance across all taxa in each functional group in each plot and dividing by total biocrust cover. Though there were nine functional groups represented in our data set (Rosentreter and Root 2019), we focused on the four most abundant groups: crustose lichens, gelatinous lichens, squamulose lichens (scale lichens), and short mosses (Fig. 3, components of each functional group described in detail in Rosentreter and Root [2019]). To better meet model assumptions, particularly linearity, we log-transformed squamulose and crustose lichen abundances. We modeled all hypothesized paths (Appendix S1: Fig. S1), including all covariances among functional groups, then reran the model without nonsignificant paths and covariances to assess fit (Grace 2006, Fig. 2B).

To explore how biocrust lichen and bryophyte communities varied among grazing intensities (objective 2), we used two species-level community analyses. We tested the multivariate differences in community composition among grazing intensities using multi-response permutation procedures with Sorensen distance (MRPP; Mielke and Berry 2007). The effect size for MRPP is expressed as A, the chance-corrected within-group agreement, which describes the within-group homogeneity and ranges from 0 to 1 (McCune et al. 2002). Indicator species analysis (Dufrêne and Legendre 1997) allowed us to test which species were most associated with low, medium, and high grazing intensity. Indicator values (IV) range from 0 to 100 with 100 being the strongest and indicating that a species is always found only in a particular grazing intensity.

Results

Biocrust cover was negatively related to grazing intensity ($F_{2,23} = 17.77$, $P < 0.0001$, Fig. 4A). Plots experiencing the lowest grazing intensity supported 46% biocrust cover on average in comparison with only 7% soil crust in the high grazing intensity plots ($P < 0.001$). Medium intensity grazing plots were intermediate, supporting 25% cover ($P = 0.01$ for the comparison with low intensity and $P = 0.025$ for the comparison with high intensity).

Similarly, biocrust species richness was negatively related to grazing intensity ($F_{2,23} = 10.80$, $P = 0.0005$, Fig. 4B). Plots with the lowest grazing intensity had the highest biocrust diversity, supporting 30 species on

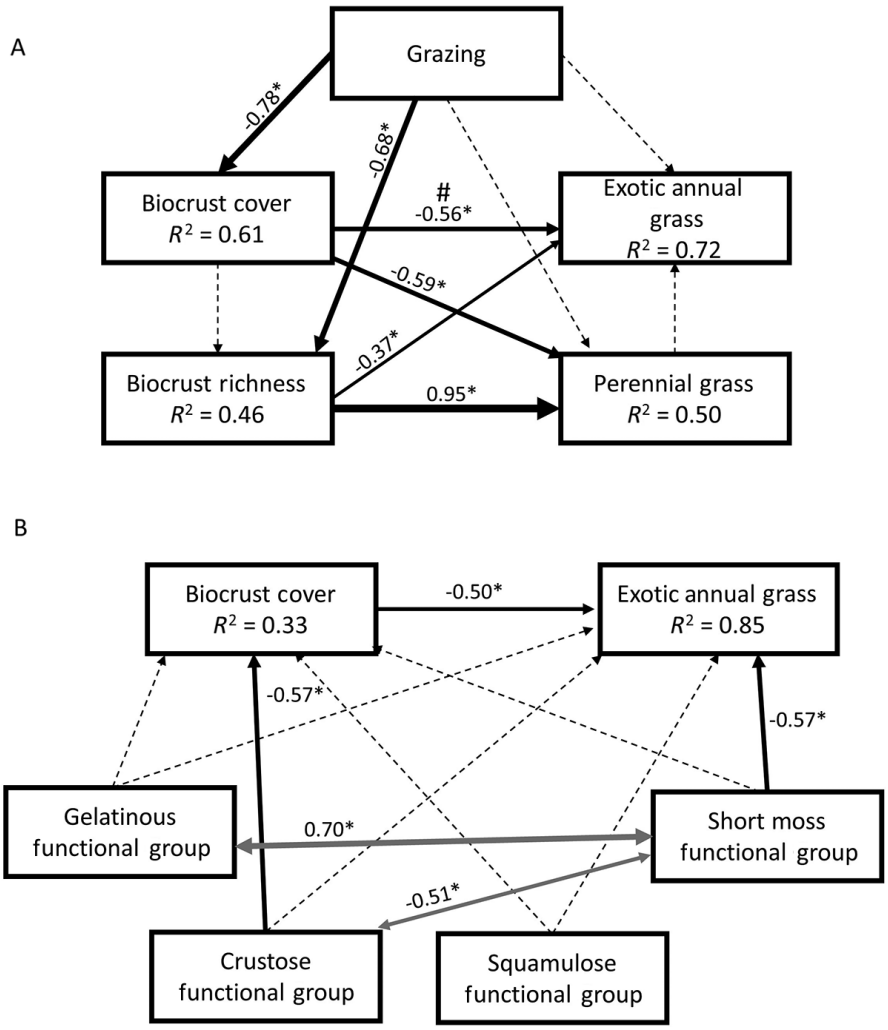


FIG. 2. Structural equation models (SEMs) testing the effects of grazing intensity on soil biocrust and vascular plant communities. These models are refined from a priori hypothesized models (Appendix S1: Fig. S1). Numbers indicate standardized path coefficients and arrow thickness is weighted by the strength of the path with their associated sign. Paths with $P < 0.05$ are labeled (*) and hypothesized paths that were not significant ($P > 0.1$) are shown as dashed black lines. (A) The first SEM examines the direct and indirect effects of grazing on exotic annual grass cover. A # marks a potential recursive path in which exotic annual grasses affect biocrust cover. (B) The second SEM examines the relative influence of individual biocrust functional groups and total soil crust cover on exotic annual grass cover. Gray double-headed arrows represent covariances.

average as compared with only 10 species on average in the high intensity grazing plots ($P = 0.0004$). Medium grazing intensity supported intermediate diversity with (on average) 24 biocrust species ($P = 0.29$ for the comparison with low intensity, $P = 0.014$ for the comparison with high intensity).

Exotic annual grasses were substantially more abundant in plots with higher grazing intensity ($F_{2,23} = 12.14$, $P = 0.0003$, Fig. 4C). Low grazing intensity plots had 1% cover of exotic annual grass compared with 58% in high intensity grazed plots ($P = 0.0002$). Medium intensity grazing did not significantly differ from low intensity (11% exotic annual grass cover, $P = 0.37$), but was significantly lower than the high intensity plots ($P = 0.005$). Perennial grasses did not significantly differ among grazing intensities ($F_{2,23} = 1.33$, $P = 0.28$, Fig. 4D). This may be due to removal of tall perennial grasses by historic grazing in winterfat and salt desert sites that are currently low or moderate grazing intensity as well as the shorter perennial grass, *Poa secunda,* not favoring sites with calcareous soils (Rosentreter and Root 2019).

SEMs indicated that grazing did not directly promote exotic annual grasses, but rather reduced biocrust cover and richness, which favored exotic annual grasses and disfavored perennial grasses (Fig. 2A). Biocrust cover negatively affected exotic annual grasses (with a path coefficient = −0.56, $P = 0.001$). This model exhibited good fit overall (P for χ^2 test = 0.76) and for

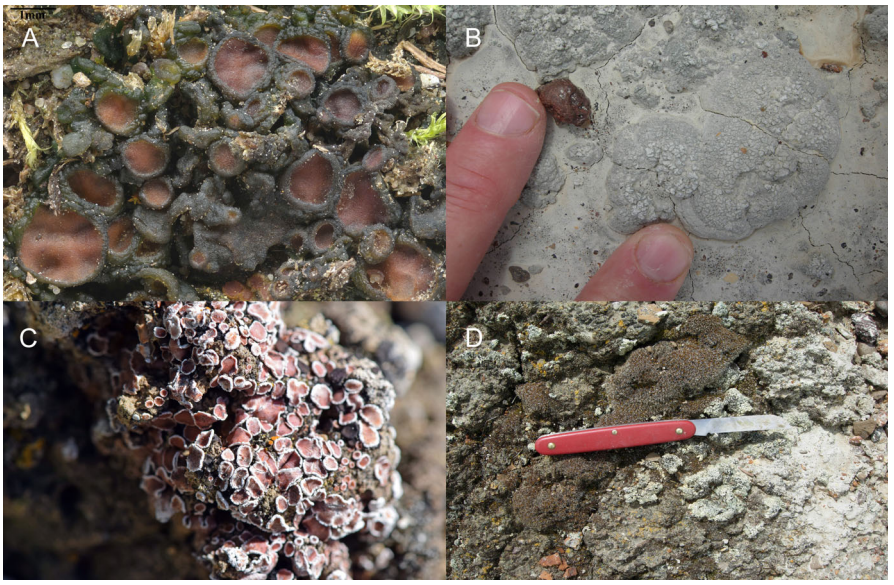


FIG. 3. Four functional groups of soil biocrusts investigated: (A) gelatinous lichen *Enchylium tenax* (A. DeBolt), (B) crustose lichen *Aspicilia* (R. Rosentreter), (C) squamulose lichen *Psora decipiens* (sometimes called scale lichens, E. K. Dodson), and (D) short moss *Syntrichia caninervis* (R. Rosentreter).

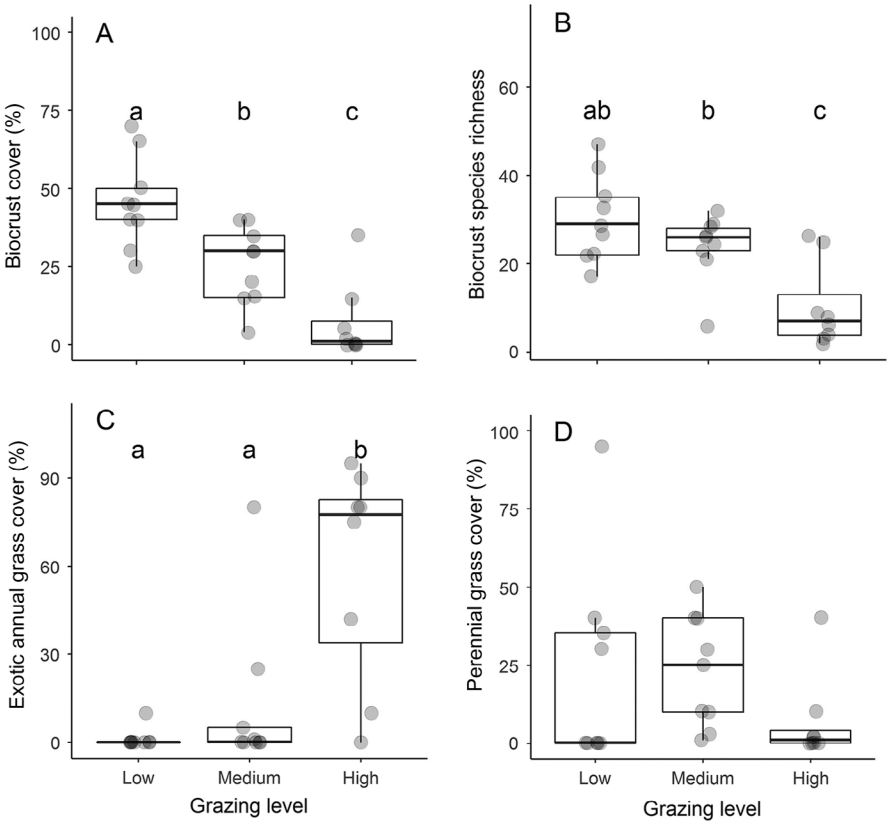


FIG. 4. Soil biocrust and vascular plants related to three levels of grazing intensity at 27 sites in Idaho, USA. Different lowercase letters indicate significantly different groups ($P < 0.05$). Box plot components are midline, median; box edges, 25th and 75th percentiles; and whiskers, 1.5 times the inter-quartile range.

each component (d-sep P all > 0.13). Covariances suggested that predictors were not so collinear as to preclude modeling (Appendix S1: Table S1). The correlation between grazing and biocrust cover (0.78) was borderline (Grace 2006) but was not of major concern because we expected this relationship and the two predictors did not co-occur in any of the final models. The post-hoc test for a reciprocal relationship between total biocrust cover and exotic annual grass cover (shown by the # in Fig. 2A and Appendix S1: Fig. S1) was not supported (path coefficient = 0.013, P = 0.968), supporting our hypothesis of biocrust cover conferring resistance to exotic annual grass invasion.

Short mosses had the strongest negative relationships with exotic annual grasses (P < 0.0001, Fig. 2B), suggesting that the loss of this functional group may precede exotic annual grass invasion. Total biocrust cover also had a negative relationship with exotic annual grasses (P < 0.0001). Crustose lichen abundance was negatively related to total biocrust cover, suggesting that this functional group is dominant when biocrust cover is poorly developed. There was no evidence that gelatinous, squamulose, or crustose lichens, as individual functional groups, were strongly related to total biocrust cover or affected exotic annual grasses directly. Crustose lichens negatively covaried with short mosses (P = 0.008) and gelatinous lichens positively covaried with short mosses (P = 0.001). As with the first SEM, model fit was good overall (P for χ^2 test = 0.15) and for each component (d-sep P all > 0.17); none of the correlations among variables was unacceptably high (Appendix S1: Table S2). This model explained 33% of the variance in biocrust cover and 85% of the variance in exotic annual grass cover.

Biocrust community composition differed among grazing intensities (MRPP A = 0.085, P = 0.001). Low and high intensity had the most different biocrust communities (P = 0.0009); low and medium intensity were not significantly different (P = 0.16), whereas medium and high intensity grazing also differed (P = 0.018). Indicator species of biocrust lichen and bryophytes were only found for the lowest grazing intensity. These included *Acarospora schleicheri* (IV = 45, P = 0.033), *Arthonia glebosa* (IV = 65, P = 0.002), *Aspicilia filiformis* (IV = 51, P = 0.013), *Aspicilia mansourii* (IV = 50, P = 0.002), *Enchylium tenax* (IV = 49, P = 0.0002), *Endocarpon loscosii* (IV = 53, P = 0.006), *Myriolecis flowersiana* (IV = 56, P = 0.004), *Placidium squamulosum* (IV = 46, P = 0.031), *Syntrichia ruralis* (IV = 48, P = 0.004), and *Chromatochlamys muscorum* (IV = 55, P = 0.003). No biocrust lichen or bryophyte species were associated most strongly with medium or high intensity grazing, suggesting that there are not species of lichens or bryophytes in the local species pool that are favored by livestock grazing.

Discussion

Our study highlights the importance of biocrust cover in maintaining site resistance to invasion by exotic annual grasses. Importantly, we show some of the first evidence that effects of biocrusts on plant germination and establishment documented by smaller-scale experimental studies (Serpe et al. 2006, 2008, Deines et al. 2007, Peterson 2013, Slate et al. 2018) appear to scale up to determine landscape-scale plant community dynamics. Specifically, since many invaders are successful because of their abundant, fast-establishing seeds (Williamson 1999), restricting their success at the seedling life stage is likely to be critical in maintaining native-dominated ecosystems. We also present some of the first quantitative evidence that different biocrust functional groups may have unique ecological roles in maintaining native plant communities. These findings are particularly important because biocrust communities, which are small in stature and difficult to identify, are rarely explicitly examined in studies of invasion ecology (Chambers et al. 2014, Bradley et al. 2018, Seipel et al. 2018, St Clair and Bishop 2019), despite previous evidence for a negative relationship between exotic annual grasses and biocrusts (Peterson 2013, Reisner et al. 2013). Since biocrusts are ubiquitous in arid and semiarid habitats (Belnap et al. 2016) that are at high risk of invasion by exotic annual grasses (Suring et al. 2005), these findings are potentially consequential for dry grassland ecosystems around the world.

The finding that biocrusts inhibit exotic plant invasion initially seems to contrast with evidence that exotic annual grasses suppress biocrusts with their litter (Hilty et al. 2004, Dettweiler-Robinson et al. 2013). Though we did not measure litter, the reciprocal pathway from exotic annual grasses to biocrust cover was not supported in our analyses. This apparent paradox may be due to different processes governing resistance to invasion as compared with resilience as sites recover from invasion (Chambers et al. 2014). Disturbances at uninvaded sites may reduce resistance by decreasing biocrust cover and facilitating annual grass invasion. After the initial invasion, annual grasses may be able to suppress remnant biocrusts, limiting resilience of the ecosystem to recover to a native-dominated community (Dettweiler-Robinson et al. 2013, Peterson 2013). Comparing these processes requires access to both relatively intact and degraded habitats; we were able to take advantage of areas that limit livestock grazing and contain well-developed biocrust communities. It is also possible that different types of disturbance such as wildfire or differing propagule pressure change the dynamic between exotic annual grasses and biocrusts. Because livestock grazing, wildfire, and exotic annual grasses co-occur throughout our study region, the effects of these ecosystem pressures can be difficult to untangle.

Our study is unique in evaluating the full diversity and community composition of biocrusts in the context of invasion at a landscape scale, and this allowed us to observe specific effects of short mosses on resistance to invasion and that particular biocrust species can be impacted by disturbance differently from others within

the same functional group. Biocrusts form diverse and functionally complex communities and reducing this complexity to measures of total percent cover, as much previous research has, may obscure the varied roles biocrusts play in ecosystems (Read et al. 2008, Miller and Damschen 2017). For example, biocrust functional guilds may have unique effects on vascular plant seed germination and establishment. The thick crustose lichen *Diploschistes muscorum* can have a stronger negative effect on germination than a mixed-species biocrust (Deines et al. 2007) and short mosses can have more of an effect than tall mosses (Serpe et al. 2006). Short mosses were particularly important in preventing exotic annual grass invasion in our study; they may be valuable in providing a fairly thick continuous layer over the soil that prevents establishment (Condon and Pyke 2018). Other studies examining biocrust communities at landscape scales have found that their diversity and composition varies greatly (Root and McCune 2012, Rosentreter et al. 2016, Root et al. 2017), which is likely to create a patchwork of varying site resistance to invasion. Since biocrust diversity and the abundance of particular species were negatively affected by grazing intensity here, maintaining taxonomically and functionally diverse biocrust communities will likely require limiting disturbance (Ponzetti et al. 2007, Root et al. 2017).

Restoring a high overall cover and diversity of biocrust species, as well as the short moss functional group in particular, may enhance ecosystem resistance to invasion. Biocrust restoration is now viewed as a critical management practice in some arid and semiarid regions (Bowker 2007), and although there has been substantial progress in developing biocrust restoration practices, significant challenges remain (Doherty et al. 2015, Condon and Pyke 2016, Bowker et al. 2017). Recent developments in growing short mosses for restoration purposes (Bowker et al. 2017) seem especially promising in light of our study, because short mosses were particularly valuable in preventing cheatgrass invasion and can be among the first to colonized disturbed soils (Read et al. 2011). However, the limited ability to grow a diversity of lichens in bulk (Bowker et al. 2017) restricts active restoration of a full biocrust community. Our results highlight the value of developing cultivation methods for short mosses, and suggest that future restoration work will benefit by developing methods to cultivate more diverse biocrust communities and improve their establishment following applications in the field.

Conclusions

The role biocrusts play in invasion dynamics has been largely overlooked but may be a critical component of site resistance (Slate et al. 2018). While the cover of biocrusts as a whole is sometimes considered in invasion studies (Reisner et al. 2013), community composition and diversity of biocrusts is rarely considered, despite their role in providing resistance to invasion. In one of the first landscape-scale studies of the interplay between biocrusts and exotic annual grasses, we highlight the importance of biocrust diversity and the abundance short mosses in determining plant communities. These findings help prioritize management in places where site resistance can be maintained, and direct biocrust restoration efforts particularly with a focus on the functional groups that are most effective at promoting site resistance. Arid ecosystems face many pressures from invasive plants, development, disturbance, and changing precipitation regimes. As climate change has been shown to impact biocrust communities in ways similar to disturbance (Ferrenberg et al. 2015), determining how stressors on biocrusts will affect plant communities remains a question of critical importance.

Acknowledgments

We would like to thank Bruce McCune, Othmar Bruess, and Rob Smith who graciously identified and verified several biocrust specimens. Ann DeBolt provided invaluable assistance and recommendations on the processing of the many plant specimens. We would also like to thank James Smith and the Snake River Plain Herbarium at Boise State University for storing most of the voucher collections associated with this project. We thank Matthew Bowker and one anonymous reviewer for constructive comments that substantially improved the manuscript.

Literature Cited

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531–556.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19:173–183.

Belnap, J., and B. Büdel. 2016. Biological soil crusts as soil stabilizers. Pages 305–320 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Belnap, J., B. Weber, and B. Büdel. 2016. Biological soil crusts as an organizing principle in drylands. Pages 3–13 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Boeken, B. R. 2018. Competition for microsites during recruitment in semiarid annual plant communities. Ecology 99:2801–2814.

Bowker, M. A. 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restoration Ecology 15:13–23.

Bowker, M. A., F. T. Maestre, and C. Escolar. 2010. Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils. Soil Biology and Biochemistry 42:405–417.

Bowker, M. A., A. J. Antoninka, and R. A. Durham. 2017. Applying community ecological theory to maximize productivity of cultivated biocrusts. Ecological Applications 27:1958–1969.

Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M. N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western

United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20:1493–1506.

Brodo, I. M., S. D. Sharnoff, and S. Sharnoff. 2001. Lichens of North America. Yale University Press, New Haven, Connecticut.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375.

Condon, L. A., and D. A. Pyke. 2016. Filling the interspace—restoring arid land mosses: source populations, organic matter, and overwintering govern success. Ecology and Evolution 6:7623–7632.

Condon, L. A., and D. A. Pyke. 2018. Fire and grazing influence site resistance to Bromus tectorum through their effects on shrub, bunchgrass and biocrust communities in the Great Basin (USA). Ecosystems 21:1416–1431.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 967–985.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Deines, L., R. Rosentreter, D. J. Eldridge, and M. D. Serpe. 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 295:23–35.

Dettweiler-Robinson, E., J. D. Bakker, and J. B. Grace. 2013. Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe. Journal of Arid Environments 94:96–104.

Doherty, K. D., A. J. Antoninka, M. A. Bowker, S. V. Ayuso, and N. C. Johnson. 2015. A novel approach to cultivate biocrusts for restoration and experimentation. Ecological Restoration 33:13–16.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Ferrenberg, S., S. C. Reed, and J. Belnap. 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. Proceedings of the National Academy of Sciences USA 112:12116–12121.

Grace, J. B. 2006. Structural equation modeling and natural systems. University Press, Cambridge, UK.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Hilty, J. H., D. J. Eldridge, R. Rosentreter, M. C. Wicklow-Howard, and M. Pellant. 2004. Recovery of biological soil crusts following wildfire in Idaho. Journal of Range Management 89–96.

Housman, D. C., H. H. Powers, A. D. Collins, and J. Belnap. 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. Journal of Arid Environments 66:620–634.

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Levine, J. M., E. Pachepsky, B. E. Kendall, S. G. Yelenik, and J. H. R. Lambers. 2006. Plant–soil feedbacks and invasive spread. Ecology Letters 9:1005–1014.

Liu, H., X. Han, L. Li, J. Huang, H. Liu, and X. Li. 2009. Grazing density effects on cover, species composition, and nitrogen fixation of biological soil crust in an inner Mongolia steppe. Rangeland Ecology and Management 62:321–327.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

McCune, B., and R. Rosentreter. 2007. Pages 1–105 *in* Biotic Soil Crust Lichens of the Columbia Basin. Monographs in North American Lichenology. Volume 1. Northwest Lichenologists, Corvallis, Oregon, USA.

McCune, B., J. Dey, J. Peck, D. Cassell, K. Heiman, S. Will-Wolf, and P. Neitlich. 1997. Repeatability of community data: species richness versus gradient scores in large-scale lichen studies. Bryologist 100:40–46.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., E. A. Holt, P. N. Neitlich, T. Ahti, and R. Rosentreter. 2009. Macrolichen diversity in Noatak National Preserve, Alaska. North American Fungi 4:1–22.

Mielke, P. W., and K. J. Berry. 2007. Permutation methods: a distance function approach. Springer Science & Business Media, New York, NY.

Miller, J. E. D., and E. I. Damschen. 2017. Biological soil crust cover is negatively related to vascular plant richness in Ozark sandstone glades. Journal of the Torrey Botanical Society 144:170–178.

Miller, J. E., E. I. Damschen, S. P. Harrison, and J. B. Grace. 2015. Landscape structure affects specialists but not generalists in naturally fragmented grasslands. Ecology 96:3323–3331.

Pando-Moreno, M., V. Molina, E. Jurado, and J. Flores. 2014. Effect of biological soil crusts on the germination of three plant species under laboratory conditions. Botanical Sciences 92:273–279.

Pechanec, J. F., G. D. Pickford, and G. Stewart. 1937. Effects of the 1934 drought on native vegetation of the Upper Snake River Plans, Idaho. Ecology 18:490–505.

Peterson, E. B. 2013. Regional-scale relationship among biological soil crusts, invasive annual grasses, and disturbance. Ecological Processes 2:2.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–66.

Ponzetti, J. M., and B. P. McCune. 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. Bryologist 104:212–225.

Ponzetti, J. M., B. McCune, and D. A. Pyke. 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin. Washington. Bryologist 110:706–722.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, C. F., D. H. Duncan, P. A. Vesk, and J. Elith. 2008. Biological soil crust distribution is related to patterns of fragmentation and landuse in a dryland agricultural landscape of southern Australia. Landscape Ecology 23:1093–1105.

Read, C. F., D. H. Duncan, P. A. Vesk, and J. Elith. 2011. Surprisingly fast recovery of biological soil crusts following livestock removal in southern Australia. Journal of Vegetation Science 22:905–916.

Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of

endangered sagebrush steppe ecosystems. Journal of Applied Ecology 50:1039–1049.

Root, H. T., and B. McCune. 2012. Regional patterns of biological soil crust lichen species composition related to vegetation, soils, and climate in Oregon, USA. Journal of Arid Environments 79:93–100.

Root, H. T., J. C. Brinda, and E. K. Dodson. 2017. Recovery of biological soil crust richness and cover 12–16 years after wildfires in Idaho, USA. Biogeosciences 14:3957–3969.

Rosentreter, R., and H. T. Root. 2019. Biological soil crust diversity and composition in southwest Idaho, USA. Bryologist 122:10–23.

Rosentreter, R., D. J. Eldridge, M. Westberg, L. Williams, and M. Grube. 2016. Structure, composition, and function of biocrust lichen communities. Pages 121–138 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Seipel, T., L. J. Rew, K. T. Taylor, B. D. Maxwell, and E. A. Lehnhoff. 2018. Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. Applied Vegetation Science 21:385–394.

Serpe, M. D., J. M. Orm, T. Barkes, and R. Rosentreter. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecology 185:163–178.

Serpe, M. D., S. J. Zimmerman, L. Deines, and R. Rosentreter. 2008. Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 303:191–205.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Slate, M. L., R. M. Callaway, and D. E. Pearson. 2018. Life in interstitial space: Biocrusts inhibit exotic but not native plant establishment in semi-arid grasslands. Journal of Ecology 107:1317–1327.

St Clair, S. B., and T. B. Bishop. 2019. Loss of biotic resistance and high propagule pressure promote invasive grass-fire cycles. Journal of Ecology. https://doi.org/10.1111/1365-2745.13156

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. Ecology 30: 58–74.

Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Pages 114–149 *in* M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. Habitat threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Williams, W. J., D. J. Eldridge, and B. M. Alchin. 2008. Grazing and drought reduce cyanobacterial soil crusts in an Australian Acacia woodland. Journal of Arid Environments 72:1064–1075.

Williamson, M. 1999. Invasions. Ecography 22:5–12.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2016/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2s7g00v.

Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Livestock grazing limits beaver restoration in northern New Mexico

Brian A. Small[1,2], Jennifer K. Frey[1,3], Charlotte C. Gard[4]

The North American beaver (*Castor canadensis*) builds dams that pond water on streams, which provide crucial ecological services to aquatic and riparian ecosystems and enhance biodiversity. Consequently, there is increasing interest in restoring beavers to locations where they historically occurred, particularly in the arid western United States. However, despite often intensive efforts to reintroduce beavers into areas where they were severely reduced in numbers or eliminated due to overharvesting in the eighteenth and nineteenth centuries, beavers remain sparse or missing from many stream reaches. Reasons for this failure have not been well studied. Our goal was to evaluate certain biotic factors that may limit the occurrence of dam-building beavers in northern New Mexico, including competitors and availability of summer and winter forage. We compared these factors at primary active dams and at control sites located in stream reaches that were physically suitable for dam-building beavers but where none occurred. Beaver dams mostly occurred at sites that were not grazed or where there was some alternative grazing management, but were mostly absent at sites within Forest Service cattle allotments. Results indicated that cattle grazing influenced the relation between vegetation variables and beaver presence. The availability of willows (*Salix* spp.) was the most important plant variable for the presence of beaver dams. We conclude that grazing by cattle as currently practiced on Forest Service allotments disrupts the beaver-willow mutualism, rendering stream reaches unsuitable for dam-building beavers. We recommend that beaver restoration will require changes to current livestock management practices.

Key words: beaver dams, *Castor canadensis*, cattle, competition, habitat requirements, riparian, *Salix*, willow

Implications for Practice

- Dam-building beavers mostly occurred where no livestock grazing was allowed and were rare on Forest Service allotments grazed by cattle.
- Restoration of beavers will require managing livestock grazing in ways that will promote abundant willows.
- On severely degraded or entrenched streams, restoration of riparian habitats and beavers may require additional efforts, such as planting suitable vegetation and installing structures that can help reconnect streams with their floodplains.

Introduction

Riparian corridors serve as "keystone" habitats in arid and semi-arid landscapes and they are one of the most productive habitat types in the western United States (Patten 1998; Stromberg et al. 2013). It is estimated that 90% of the original riparian habitat in New Mexico and Arizona has been destroyed or severely degraded (Ohmart & Anderson 1986). In addition, studies have predicted that increases in global temperatures will cause an increase in the intensity of winter flood events and increases in the duration and severity of drought conditions, particularly in the western United States (Seager et al. 2007; Dominguez et al. 2012). Consequently, there is heightened need for methods that will restore riparian habitats and associated aquatic environments, and that will contribute to the resilience of these systems in the face of a changing climate, particularly with respect to water conservation.

Castor canadensis (North American beaver; hereafter beaver) historically occurred in nearly all perennial streams throughout the American Southwest (Weber 1971; Findley et al. 1975). In small- to medium-sized streams beavers construct dams that pond water, which provides concealment cover from predators (Müller-Schwarze & Sun 2003). Beaver dams have far-reaching ecological effects due to factors such as storage of precipitation and seasonal runoff, decrease in stream flow velocity, which results in a decrease of bank erosion, and an increase in nutrient cycling rate (Gurnell 1998; Rosell et al. 2005; Andersen et al. 2011; Pollock et al. 2014). Beavers are also considered a keystone species because their dams cause

Author contributions: JKF conceived the research; BAS, JKF designed the research; BAS collected the data; BAS, JKF, CCG analyzed the data and wrote the manuscript.

[1]Department of Fish, Wildlife, and Conservation Ecology, New Mexico State University, Las Cruces, NM 88003-8001, U.S.A.
[2]Present address: U.S. Fish and Wildlife Service, Arlington Ecological Services Field Office, Arlington, TX 76006, U.S.A.
[3]Address correspondence to J. K. Frey, email jfrey@nmsu.edu
[4]Department of Economics, Applied Statistics & International Business, New Mexico State University, Las Cruces, NM 88003-8001, U.S.A.

© 2016 Society for Ecological Restoration
doi: 10.1111/rec.12364
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12364/suppinfo

an increase in biodiversity, particularly riparian and aquatic obligates (Naiman et al. 1993; Rosell et al. 2005; Stoffyn-Egli & Willison 2011).

During the eighteenth and nineteenth centuries, beavers were intensively harvested for their pelts, resulting in severely reduced populations and extirpation from many streams (Albert & Trimble 2000; Baker & Hill 2003; Fouty 2003; Carrillo et al. 2009). Although laws have since been enacted to protect beavers from overharvesting and there were intensive efforts to reintroduce populations during the mid 1900s, beaver populations remain low in many regions of the arid west and they have not reoccupied many smaller order streams where they historically occurred (Huey 1956; Baker & Hill 2003). For instance, though historical and current beaver populations are difficult to estimate, it has been estimated that the current beaver population in New Mexico is one sixth the size of the historical population with many stream reaches still unoccupied (Wild 2011; WildEarth Guardians 2013). Reasons why beavers have not recolonized historically occupied streams in the American West have not been well studied. Presumably, this relates to some aspect of habitat quality, given that successful beaver restorations supplemented vegetation or targeted areas with abundant vegetation (e.g. Apple et al. 1985; Albert & Trimble 2000; Pollock et al. 2015). Most studies on habitat requirements of beavers have been conducted in ecoregions with different habitat types than found in the arid west (Baker & Hill 2003). There is increasing interest in restoring populations of dam-building beavers in the western United States because of their positive effects on aquatic and riparian habitats (Keller 2014; Pollock et al. 2014, 2015) and as a means to mitigate impacts of climate change on stream systems and aquatic resources (Hood & Bayley 2008*a*; Bird et al. 2011; Wild 2011; Pollock et al. 2015).

The ability of beavers to build and maintain dams on a stream reach is limited by physical aspects of the reach. Stream flow must be great enough to allow for ponded deep water year-round, but also low enough that dams are not frequently or seriously breached by floods (Macfarlane et al. in press). Thus, prior studies have found that stream gradient, stream order, and bank or valley slope are related to occurrence of beaver dams (Slough & Sadleir 1977; Howard & Larson 1985; Suzuki & McComb 1988; McComb et al. 1990; Barnes & Mallik 1997). The thresholds for these variables are not expected to vary geographically and are difficult or impossible for managers to manipulate.

In contrast, biological factors such as vegetation that influence occurrence of beavers are more easily controlled by management. Beavers are central place foragers and "choosy generalist" herbivores that rely on a few key plant species (Allen 1983; Müller-Schwarze & Sun 2003). Thus, beavers require a suitable plant association in close proximity to the pond, which is used for both food and material to build dams. Herbaceous vegetation constitutes a major portion of beavers' summer diet whereas certain woody species constitute a major portion of their winter diet (Svendsen 1980; Müller-Schwarze & Sun 2003). If suitable herbaceous food plants are limited, then woody species also can become a significant portion of the summer diet (Müller-Schwarze & Sun 2003). Woody species most commonly browsed by beavers in western North America include willows (*Salix* spp.), cottonwoods (*Populus* spp.), quaking aspen (*Populus tremuloides*), and alders (*Alnus* spp.) (Jenkins 1975; Allen 1983; Barnes & Mallik 1996).

Another biological factor that may limit the presence of beaver is competition for shared forage species by other browsers (Brookshire et al. 2002; Hood & Bayley 2008*b*). Ungulate browsing can cause the loss of willows and subsequently beaver from a stream reach. This is true for both livestock and native ungulates such as elk (*Cervus elaphus*), especially when natural predators are missing from ecosystems (Baker et al. 2005; Ripple & Beschta 2012).

Our goal was to identify biotic factors that limit the occurrence of dam-building beavers in northern New Mexico in order to provide guidance to land managers on how they can establish or enhance riparian conditions that will support beavers. Our specific objectives were to determine vegetation required by beaver for summer forage (herbaceous vegetation) and winter forage (select woody species), and to determine the influence of livestock and native ungulates on riparian vegetation and beaver occurrence. We hypothesized that occurrence of dam-building beavers would be associated with certain herbaceous plants, deciduous shrubs and trees, and grazing by livestock and elk.

Methods

Study Site Selection

Our study area was located in north-central New Mexico on lands managed by Carson and Santa Fe National Forests. This region is in the Southern Rocky Mountains. Elevations range from 1,700 to 4,000 m elevation and the Köppen–Geiger climate classification is mostly temperate continental in the mountains and cold semiarid in the surrounding lowlands (Peel et al. 2007). This area was selected because it is public land, and it has the highest density of perennial streams and known active beaver dams in New Mexico (Fig. S1, Supporting Information). However, after we collected data at all known active beaver dams within the study area, we included additional dams on nearby lands managed by the Bureau of Land Management and private land owners in order to increase the sample size. Field data were collected 15 May to 15 August 2013.

We categorized sites as present (i.e. site had an actively maintained primary dam) or absent (i.e. stream reach had physical characteristics to support construction of a beaver dam but none currently occurred). We identified the primary dam by the presence of a lodge or bank den. We determined occupancy of a site by the presence of fresh plant cuttings, fresh mud on the dam, or fresh beaver slides entering and exiting the water. Because the home range of a beaver colony typically occupies 1.0 km or less of stream length (Aleksiuk 1968), we spaced sites no closer than 1.0 km from another site on the same stream, which prevented selection of multiple dams created by one colony as separate sites. Henceforth, we refer to active primary dams as beaver dams.

We used geographic information system (GIS) to identify stream reaches that were suitable for dam construction by

beavers based on physical characteristics of the stream, including the presence of perennial water, stream order less than 5, and stream gradient less than 10% (Allen 1983; Beier & Barrett 1987; Suzuki & McComb 1988; McComb et al. 1990). Although beavers prefer lower stream gradients for building dams (e.g. ≤4%; Pollock et al. 2004), we sampled stream gradients of 0–10% to avoid excluding any potential habitat. These data were obtained from the National Hydrologic Dataset *Plus* v.2 database (http://www.horizon-systems.com/nhdplus/). We selected absence sites from within the same biotic community as presence sites, but regardless of grazing policy, based on the national land cover data (v. 2) from the National Gap Analysis Program (http://gapanalysis.usgs.gov/gaplandcover/). Within a stream reach with suitable physical characteristics for dam construction, we located the absence site at the downstream end of the lowest gradient region in order to maintain consistency and because beavers preferentially build dam on the lowest gradient reaches. We collected data at 29 beaver dams and at 28 sites where physical conditions were suitable for construction of beaver dams, but beaver dams were absent.

Field Data Collection

Plots. At each site we established a pair of 200 m primary transects that paralleled the stream (one on either side) and positioned 0.5 m inland from the greenline (i.e. the first vegetation growing next to the water). The dam (or absence site) was located midway along the primary transects. At 40 m increments along the primary transects, we established 80 m secondary transects that extended perpendicular from the primary transect into the uplands. We measured vegetation in 1.5×1.5 m–plots along these transects. Plots were located every 20 m along the primary transects to sample the shoreline vegetation. Prior studies have shown that most foraging by beavers occurs within 30 m of water's edge, with 100 m being a typical extreme distance (Allen 1983). Thus, we located plots on the secondary transects 5, 10, 20, and 80 m away from the primary transect. Each site had a total of 68 plots.

Availability of Summer Forage. We considered summer forage for beavers to consist primarily of herbaceous vegetation and leaves and twigs of riparian shrubs (Jenkins 1975, 1979). Beavers also utilize aquatic vegetation for food (Svendsen 1980), but we did not measure this aspect. To estimate the availability of summer forage, we established a 20×150 cm Daubenmire frame (Daubenmire 1959) within each plot to measure ground cover of plant groups. The Daubenmire frame was viewed from a 1 m height to estimate cover. Plant groups included sedge (*Carex* spp.), rush (*Juncus* spp.), forb, grass, cattail (*Typha* spp.), field horsetail (*Equisetum arvense*), rose (*Rosa* spp.), redosier dogwood (*Cornus sericea*), willow (*Salix* spp.), quaking aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), alder (*Alnus* spp.), juniper (*Juniperus* spp.), oak (*Quercus* spp.), bare ground, gravel/rock, and an "other" category consisting of ground cover such as woody debris, leaf litter, moss, and fecal piles. Cover classes were 0–5, 5–25, 25–50, 50–75, 75–95, and 95–100%. In addition, we measured two variables that might summarize summer forage availability, vertical cover, which is an estimate of the height of herbaceous vegetation (Robel et al. 1970) and soil moisture, which promotes growth of riparian plants. Vertical cover was measured with a Robel pole placed at the center of every frame and viewed from 1 m height and 4 m distance in two random directions (Robel et al. 1970). Soil moisture was measured within each frame using a soil moisture meter (Lincoln Irrigation Inc., Lincoln, NE, U.S.A.) inserted into the ground circa 115 cm, and ranged from 0 (dry) to 10 (saturated).

Availability of Winter Forage. We considered winter forage for beavers to consist primarily of small diameter (<5 cm) stems of woody plants that are selected by beavers disproportionately more than available (Barnes & Mallik 1996). We identified, counted, and measured the diameter of all woody plant stems (both cut and uncut by beaver) within each plot. We measured the diameter of stems 0.5 m aboveground level, which approximates the height of a foraging beaver (i.e. diameter-at-*beaver*-height; dbh), or at the tip of the ungnawed portion of the stump if it was less than 0.5 m in height.

Competitors. At our study sites, the potential herbivorous competitors of beavers included several species of native ungulates (deer [*Odocoileus* spp.], elk [*Cervus elaphus*]) and livestock (cattle, horse, sheep, American bison [*Bison bison*]; Lucas et al. 2004; Baker et al. 2005). We measured use of sites by ungulates using two methods. First, because livestock grazing is an anthropogenic factor that can occur independent of habitat characteristics, we categorized each site by livestock grazing policy: (1) grazing was not allowed (i.e. no grazing), (2) grazing by cattle was allowed and occurred via a permit within a Forest Service grazing allotment with no special provisions (i.e. Forest Service cattle allotment), or (3) grazing by livestock was allowed but was by species other than cattle (horse or bison), occurred on private land, or occurred on Forest Service land but under special treatment such as a riparian pasture or during short-term (i.e. 5 days) walk-through trailing (i.e. other grazing). Thus, we interpreted sites where grazing was allowed to reflect the potential for relatively long-term use of sites by livestock, regardless of recent unauthorized use by livestock or use by native ungulates. We obtained information on the grazing policy for each site from the land management agency or owner after all field data were collected. Second, we identified and counted all ungulate fecal piles within 1 m of secondary transects (Lancia et al. 2005) and interpreted these data as representative of the intensity of recent use by ungulates, regardless of livestock grazing policy. Fecal pile counts represent an index of relative use of an area by a given species, but counts are not directly comparable among species due to variation in detection, defecation and decomposition rates. Fecal pile counts can be influenced by observer, observation distance, vegetation characteristics, and other factors (Jenkins & Manly 2008). However, we considered our counts to have low observational bias because two observers made the counts and we only counted fecal piles in very close proximity (<1 m) to the transect line (Jenkins & Manly 2008).

Statistical Analysis

Analyses were performed using SAS 9.4 (SAS Institute, Cary, NC, U.S.A.) and Minitab 17 (Minitab Inc., State College, PA, U.S.A.). A change in field data collection methods resulted in missing data for four summer forage availability variables (percent cover of willow, alder, cottonwood, and aspen) at five sites; we imputed the missing data using linear regression. We calculated riparian width, which was tested as a potential confounder, by identifying the presence of hydrophilic species (e.g. sedge, rush, willow) in all plots on secondary transects; distances of these plots from the primary transect were averaged for the site. We used the midpoints of the cover classes to determine percent cover of plant groups for each plot. We averaged across all plots within each site to obtain site-level variables for analysis, except for fecal counts, which were averaged across all secondary transects, and livestock grazing policy, which was categorical. We tested data for normality with Kolmogorov–Smirnov tests. We tested variables for differences between presence and absence sites using two-tailed *t*-tests for normally distributed variables and Mann–Whitney *U*-tests for non-normally distributed variables (Table S1).

Grazing by livestock and native ungulates can have a strong influence on the composition and structure of riparian vegetation (Kauffman et al. 1983; Singer et al. 1994; Brookshire et al. 2002; Holland et al. 2005; Batchelor et al. 2014). Consequently, we explicitly considered competitor variables as potential confounders on the relations between plant variables and presence or absence of beaver dams. Confounding occurs when the relation between the plant variable and presence or absence of a beaver dam is distorted by a third variable (i.e. a competitor) that is associated with both the plant variable and the presence or absence of a beaver dam. We evaluated the extent of confounding by grazing policy on each vegetation variable by calculating the percent change in the odds ratio of the crude relation and the odds ratio of the adjusted relation when controlled for grazing policy (Rosner 2000); we considered a 10% change to indicate significant confounding (Greenland 1989).

We developed logistic regression models to predict presence or absence of beaver dams based on each of the biotic driver categories (i.e. competitors, summer forage availability, winter forage availability). For developing the competitor and summer forage availability models, the initial pool of variables included those that were significant at p less than or equal to 0.20 in the univariate tests. Because we had data on stems that were both cut and uncut by beavers, for the winter forage availability model, we used a different process to narrow the suite of variables to only species that were selected by beavers. Using data only from presence sites, we calculated diet selection using a standardized resource selection index B, which is a probability ranging from 0 to 1 that a food item will be selected if all types are equally available (Manly et al. 2002): for each of the 21 available woody plant species, $B = \left(\frac{u}{a}\right) / \Sigma \left(\frac{u}{a}\right)$, where u is the proportion of cut stems and a is the proportion of cut plus uncut stems. Selection for or against a plant is indicated by a value of B greater or less than 0.048 respectively (i.e. $1/n$ where $n = 21$, the number of available small diameter woody plant species; Manly et al. 2002).

Our modeling followed the "purposeful selection" approach of Bursac et al. (2008). Purposeful selection allows for variables known to be biologically important to be tested during model development, that otherwise would be removed from consideration due to statistical insignificance (Bursac et al. 2008). Although multimodel inference and information theory have become a favored approach in the analysis of ecological data (Burnham & Anderson 2002), we considered purposeful selection a superior method for these analyses because it allowed us to identify and incorporate variables that had a confounding effect on statistically significant variables. This permitted explicit inclusion of the most influential competitor variables as potential confounders within the vegetation models. First, a logistic regression model was created that used the initial pool of variables (plus potential competitor confounders) for each biotic driver category. The variable with the highest p was removed and a new model constructed based on the remaining variables. We evaluated significance at p greater than or equal to 0.10 due to small sample sizes and large variation inherent to natural communities. Thus, variables were removed in this way until no variables remained with p greater than or equal to 0.10. During this process of variable removal, we tested each removed variable to determine if it was a confounder on the remaining variables. Bursac et al. (2008) recommended identifying a variable as a confounder if, when the variable of interest was removed, the beta coefficient of any of the remaining variables in the model changed by more than 15–20%. We used a more stringent criterion, requiring a 25% or greater change in the beta coefficient; this assured we identified only the most strongly confounding variables. Variables found to be confounders were retained. Secondly, variables that did not make the initial pool of variables (i.e. p greater than or equal to 0.20 in univariate tests for the summer forage availability and competitors models; woody species unused or avoided by beaver for the winter food availability model) were included in the model one at a time in order to determine if the variable became significant ($p < 0.10$) in the presence of the other variables. Any variables identified as significant were retained and the iterative process was repeated for the variables added. Lastly, a final global model was created using the same iterative process of purposeful selection, but utilizing the final variables in each of the biotic driver models as the initial pool of variables. We tested select interactions with livestock grazing policy in the final global model including percent ground cover by grasses, forbs, and willows, and number of willow stems in the regeneration size class (dbh < 5 cm). Due to the potential for issues with multicollinearity, we required that all variables in final models have a variance inflation factor ≤ 2.5 (Allison 1999).

Results

The final model of competitors contained only livestock grazing policy (Table 1). Odds of an active beaver dam at sites with no grazing was 37.3 (90% CI [8.76, 159.11]) times the odds at

Table 1. Coefficients of determination, beta coefficients, odds ratios, and *p*-values for the biotic driver models and the final global models at sites with an active beaver dam present ($n = 29$) or absent ($n = 28$). [a]Non-significant variables in univariate testing: elk (*Cervus elaphus*), deer (*Odocoileus* spp.), American bison (*Bison bison*), horse (*Equus caballus*). [b]Significant variables removed during multivariable testing: bare ground/rock, percent rush (*Juncus* spp.), percent cattail (*Typha* spp.; non estimable), percent oak (*Quercus* spp.; non-estimable), percent cottonwood (*Populus* spp.), percent redosier dogwood (*Cornus sericea*; non-estimable), mean vertical cover, soil moisture, riparian width. [c]Non-significant variables in univariate testing: percent field horsetail (*Equisetum arvense*), percent juniper (*Juniperus*), percent sedge (*Carex* spp.), percent grass, percent forb, percent rose (*Rosa* spp.), percent alder (*Alnus* spp.), percent quaking aspen (*Populus tremuloides*). [d]Riparian width was tested as a potential confounder. [e]Significant variable removed during multivariable testing: redosier dogwood (non-estimable). [f]Canopy cover and riparian width were tested as potential confounders; juniper stems and oak stems were tested for significance in the final winter forage model. [g]NE indicates a non-estimable value (>999.99) due to the narrow range of sampling. [h]Retained as a confounder on other grazing policy.

Model	r^2	*Beta Coefficient*	*Standardized Beta Coefficient*	*Odds Ratio*	*90% Confidence Interval*	*p Value*
Competitor[a]	0.384					
Grazing policy						<0.001
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		2.86	—	17.50	4.29–71.41	0.001
No grazing		3.62	—	37.33	8.76–159.11	<0.001
Competitor (without livestock grazing policy)	0.173					
Cattle fecal piles		−0.25	−0.605	0.78	0.67–0.91	0.007
Summer forage[b,c,d]	0.421					
Percent willow (*Salix* spp.) ground cover		0.76	0.570	2.13	0.97–4.68	0.114
Grazing policy						0.004
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		2.53	—	12.62	2.95–53.94	0.004
No grazing		2.77	—	15.91	3.23–78.28	0.004
Winter forage[e,f] (=global model A)	0.614					
Willow stems		1.12	2.866	3.07	1.45–6.47	0.014
Alder (*Alnus* spp.) stems		3.02	0.951	20.43	2.20–190.11	0.026
Quaking aspen (*Populus tremuloides*) stems		8.78	1.365	NE[g]	12.77–NE	0.021
Cottonwood (*Populus* spp.) stems		5.64	1.460	282.27	3.20–NE	0.038
Boxelder (*Acer negundo*) stems		5.15	0.390	172.57	0.07–NE	0.277[h]
Grazing policy						0.032
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		5.67	—	291.18	8.23–NE	0.009
No grazing		1.13	—	3.10	0.16–59.79	0.530
Global model B	0.526					
Percent willow (*Salix* spp.) ground cover		1.07	0.810	2.93	1.19–7.22	0.050
Alder (*Alnus* spp.) stems		2.12	0.668	8.33	1.52–45.77	0.041
Quaking aspen (*Populus tremuloides*) stems		4.18	0.650	65.50	1.62–NE	0.063
Cottonwood (*Populus* spp.) stems		2.50	0.646	12.17	1.27–116.42	0.069
Grazing policy						0.011
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		3.64	—	37.96	4.79–300.71	0.004
No grazing		3.69	—	39.89	3.78–421.34	0.010

sites in Forest Service cattle allotments and the odds of an active beaver dam at sites in other grazing was 17.5 (90% CI [4.29, 71.41]) times the odds at sites in Forest Service cattle allotments. In order to determine which species of competitors were most influential, we fit a second model that excluded livestock grazing policy. This model contained only cattle (Table 1). The odds of an active beaver dam decreased by 22% (odds ratio = 0.78, 90% CI [0.67, 0.91]) for each increase of 1 in the mean number of cattle fecal piles on transects. Thirteen of 27 variables were significantly different ($p \leq 0.1$) among sites that differed by livestock grazing policy (Table S2), such that sites where livestock grazing was allowed, particularly within Forest Service cattle allotments, often resembled upland communities (Fig. 1). In addition, livestock grazing policy had a confounding effect on 15 out of 23 estimable variables (Table S3). Consequently, livestock grazing policy was tested within the summer and winter forage availability models.

The summer forage availability model reduced to one that contained only livestock grazing policy. However, the penultimate model, which also contained percent ground cover by willow ($p = 0.114$) had a lower deviance (47.78 versus 61.41) and hence was selected as the final summer forage model (Table 1). The odds of an active beaver dam increased by 113% (odds ratio = 2.13, 90% CI [0.97, 4.68]) with every 1% increase in mean willow ground cover per plot (Table 1).

Beavers selectively cut stems from six species of woody plants, including willows, alders, quaking aspen, cottonwoods, boxelder, and redosier dogwood (Table 2). The final model for winter forage availability contained livestock grazing policy and all of these plants except redosier dogwood, which could not be modeled because it did not occur at Forest Service



Figure 1. Photo of a reach of the Rio de las Vacas (English translation: River of Cows), Sandoval County, NM, U.S.A., where livestock grazing is allowed and beaver dams are absent (top); photo of a reach of the Rio Grande del Rancho, Taos County, NM, U.S.A., where livestock grazing is not allowed and beaver dams are present (bottom).

cattle allotment sites (Table 1). The standardized beta coefficients indicate that willow was the strongest contributor to this model (Table 1). The odds of an active beaver dam increased 207% (odds ratio = 3.07, 90% CI [1.45, 6.47]) for every one stem increase in mean willow per 1.5 m^2 plot and increased 1,943% (odds ratio = 20.43, 90% CI [2.20, 190.11]) for every one stem increase in mean alder per 1.5 m^2 plot; odds ratios for quaking aspen, cottonwood, and boxelder were high but had non-estimable confidence intervals (Table 1).

Due to a strong correlation ($r_s = 0.846$) between willow stems and percent willow ground cover, we developed two separate global models that each deleted one of these variables from the final pool of variables derived from the final biotic driver models. When percent willow ground cover was deleted, the final global model (A) was the same as the winter forage model. When willow stems was deleted, the final global model (B) contained livestock grazing policy, percent willow ground cover, and stems of alder, quaking aspen, and cottonwood. The odds of an active beaver dam increased 193% (odds ratio = 2.93, 90% CI [1.19, 7.22]) for every 1% increase in mean willow ground cover per plot, increased 733% (odds ratio = 8.33, 90% CI [1.52, 45.77) for every one stem increase in mean alder per 1.5 m^2 plot, and increased 1,117% (odds ratio = 12.17, 90% CI [1.27, 116.42) for every one stem increase in mean cottonwood per 1.5 m^2 plot; the odds ratio for quaking aspen was high but the confidence interval was not estimable (Table 1). Willow was the strongest contributor to this model. However, the winter forage model ($r^2 = 0.614$) provided a stronger fit of the data compared to global model B ($r^2 = 0.526$) and hence was the overall best model.

Discussion

The sparse occurrence of beaver dams found during our study was in stark contrast to the widespread historical distribution and abundance of beavers along most perennial streams in New Mexico (Bailey 1931; Weber 1971; Findley et al. 1975). Our spatial model predicted 3,021 km (1,813 miles) of streams on federal public lands in New Mexico with potentially physically suitable characteristics for the construction of beaver dams. However, although we undoubtedly overlooked some beaver dams, we found only 38 active primary beaver dams occurring on public lands in the entire state of New Mexico. Given that on average a single beaver colony occupies 1 km of stream

Table 2. Availability (*a*), utilization (*u*), and standardized resource selection index (*B*) for small diameter (<5 cm) woody plant species used as winter forage at sites with an active beaver dam ($n = 29$). [a]Selection for or against a plant is indicated by a value of *B* greater or less than 0.048, respectively. [b]Species not used by beavers: juniper (*Juniperus* spp.), pine (*Pinus* spp.), spruce (*Picea* spp.), fir (*Abies* spp.), Rocky Mountain maple (*Acer glabrum*), mulefat (*Baccharis salicifolia*), snowberry (*Symphoricarpos oreophilus*), Russian olive (*Elaeagnus angustifolia*), New Mexico locust (*Robinia neomexicana*), chokecherry (*Prunus* spp.), rose (*Rosa* spp.), gooseberry (*Ribes* spp.), and elm (*Ulmus* spp.).

Plant Species	*Proportion Available (a)*	*Proportion Utilized (u)*	*Standardized Resource Selection Index (B)*[a]	*Selection Relative to All Species*[b]
Cottonwood (*Populus* spp.)	0.037	0.054	0.209	Positive
Alder (*Alnus* spp.)	0.069	0.085	0.179	Positive
Willow (*Salix* spp.)	0.711	0.820	0.166	Positive
Boxelder (*Acer negundo*)	0.006	0.006	0.132	Positive
Quaking aspen (*Populus tremuloides*)	0.013	0.012	0.131	Positive
Redosier dogwood (*Cornus sericea*)	0.019	0.015	0.114	Positive
Big sagebrush (*Artemisi tridentata*)	0.007	0.003	0.053	Neutral
Oak (*Quercus* spp.)	0.035	0.004	0.017	Avoid

(Aleksiuk 1968), the estimated colony density of dam-building beavers was 0.01 per km of physically suitable stream reaches on public lands in New Mexico. Another recent study also found beavers to be absent from many streams predicted to be suitable in New Mexico (WildEarth Guardians 2013). In contrast, reported colony densities on streams in other areas of North America range from 0.63 to 1.90 per km (Pollock et al. 2015). Our results suggest that the widespread absence of beaver in our study area was due to the widespread absence of adequate riparian vegetation and that the absence of adequate riparian vegetation was associated with livestock grazing, particularly as typically occurs on Forest Service cattle allotments.

In our study, beavers selected several species of deciduous woody plants, including alders, boxelder, cottonwoods, quaking aspen, willows, and redoiser dogwood. Other studies also have regarded these species, especially trees in the genus *Populus* (i.e. cottonwoods and quaking aspen), as preferred forage for beavers, and these are some of the few deciduous species that occur in the arid west (Pollock et al. 2015). However, we found willows to be the most important plant for occurrence of beaver dams in our study. In contrast, other studies often identify other species of deciduous shrubs and trees as more important to beavers than willows (e.g. Müller-Schwarze & Sun 2003). For instance, in eastern North America where there is relatively high diversity of deciduous trees and shrubs, beavers selectively forage on a wide range of other deciduous species, typically preferentially to willows (Fryxell & Doucet 1993; Doucet et al. 1994; Gallant et al. 2004). In those systems, high woody plant diversity may buffer competition between beavers and ungulates for overlapping resources (Hood & Bayley 2008*b*). In contrast, in the arid west there are fewer species of deciduous trees and shrubs, which places relatively greater pressure on the few species present. Although other species might be preferred more than willows, we attribute the overriding importance of willows in our study to the relative scarcity of other species in our study area. For instance, willows represented 71.1% of available woody stems found at dam sites, whereas alders, boxelder, cottonwoods, aspen, and dogwood accounted for less than 15% of available woody stems combined.

In western North America and other locations, beavers and willows exhibit a mutualism wherein beavers are benefitted via the food and building material provided by willows whereas willows benefit from beavers via the increase in wetland area created by dams, vigorous resprouting stimulated by beaver foraging, and reproduction of limbs cut by beavers (e.g. Kindschy 1989; Peinetti et al. 2009). However, browsing on willows by livestock or native ungulates can disrupt this mutualism by causing a decrease in willow biomass and thus a decrease in the suitability of an area for beavers (Kindschy 1989; Singer et al. 1994; Brookshire et al. 2002; Baker et al. 2005, 2012). Studies in national parks where livestock are not allowed found that elk are capable of disrupting the beaver-willow mutualism (Baker et al. 2005, 2012; Ripple & Beschta 2012). In contrast, in our study elk fecal piles were not an important predictor of beaver dam occurrence, and they were not highly correlated with any vegetation variable. In Yellowstone National Park, it was not until gray wolves (*Canis lupus*) were restored that woody species such as willow, aspen, and cottonwood showed an increase in growth rate and height (Ripple & Beschta 2012). Baker et al. (2012) found that in a simulated montane willow ecosystem within Rocky Mountain National Park, beavers persisted indefinitely when elk density was less than or equal to 20 elk per km^2 and persistence decreased exponentially as elk density increased beyond 30 elk per km^2. In contrast, the north-central elk herd in New Mexico has an estimated mean density of 2.2-2.3 elk per km^2 (N.A. Quintana 2015, New Mexico Department of Game and Fish, personal communication). Although density estimates are imprecise and locally higher densities occur in more favorable habitat and during certain seasons, the current estimated density of elk in most of our study area was well below the threshold found by Baker et al. (2012). Thus, we suggest that competition for willow by cattle and beaver is the likely mechanism that explains our statewide and regional patterns of beaver exclusion where grazing policies allow unrestricted access of cattle to riparian areas.

In conclusion, we found that beaver dams were exceptionally rare on public lands managed for cattle grazing. Large numbers of cattle and other livestock were first introduced to northern New Mexico by Spanish explorers and colonists during the late sixteenth century, predating even the establishment of the first English colony (Jamestown) along the eastern seaboard (Bowling 1941). In contrast, although cattle were introduced to some localized areas of southern Texas, Arizona, and California during the seventeenth and eighteenth centuries, cattle did not reach most parts of the West until the open range cattle boom, which followed the Civil War and expansion of the railroad system during the mid to late nineteenth century (Love 1916). Thus, livestock have been part of the landscape of northern New Mexico for circa 300 years prior to their introduction to many other regions of the West. Given the long period of time that livestock grazing has occurred in northern New Mexico, this region could serve as a harbinger for potential future conditions in other arid regions of the western United States, unless efforts are made to prevent and reverse any long-term detrimental effects of livestock grazing on riparian habitats.

Our results indicate that reestablishment of beavers in northern New Mexico, and likely elsewhere in many areas of the arid montane west where livestock management is similar, must involve the restoration of riparian woody plant communities, especially abundant willows. However, our results suggest that restoration of willows will often require changing grazing management. The net impact of cattle grazing on riparian habitat is a function of the number of cattle and timing of grazing. In our study area, most Forest Service cattle allotments have utilization rates for the uplands based on the conservative grazing intensity guidelines of Holecheck and Galt (2000) with use during the growing season (generally May or June depending on elevation through mid-October). Riparian zones within these allotments usually are not fenced and have no special grazing management other than a designated herbaceous utilization rates, typically 10 cm stubble height (F.E. Cortez 2016, Carson National Forest, personal communication). Rest may be used to offset adverse conditions or overutilization. However, in degraded habitats (such as found throughout most our study area) it may require

more than a decade of nonuse to initiate recovery (Belsky et al. 1999). Consequently, complete removal of livestock from riparian zones, either via fenced exclosures or closing grazing allotments, is recommended to improve riparian habitats (Belsky et al. 1999). Indeed, the success of exclusion at restoring willows and other riparian vegetation is well-documented (e.g. Rickard & Cushing 1982; Schulz & Leininger 1990; Case & Kauffman 1997; Belsky et al. 1999; Brookshire et al. 2002; Hough-Snee et al. 2013).

The use of alternative controlled grazing strategies to benefit riparian habitats is generally less understood, more variable, and may not result in as much recovery as exclusion (e.g. Lucas et al. 2004). Cattle grazing during the mid- to late-growing season is particularly harmful to willows because grasses become less palatable than willows as they mature (Kovalchik & Elmore 1992; Pelster et al. 2004). Pelster et al. (2004) found that in willow-sedge habitats during fall, willows comprised greater than 20% of steer diets even at low utilization rates (15%; stubble height = 37 cm). They suggested that stubble height $\geq$ 20 cm may be necessary to minimize willow consumption by cattle in Rocky Mountain willow-sedge communities (Pelster et al. 2004). However, similar research has not been conducted in other riparian habitats. Consequently, cattle grazing restricted to the spring period, with close monitoring of utilization, may reduce browsing on willows, albeit less so than exclusion (Clary 1999; Pelster et al. 2004; Booth et al. 2012). More recently, Freitas et al. (2014) found that tightly controlled grazing based on riparian standards (herbaceous utilization < 35%, willow utilization < 20%, and streambank damage < 10%) resulted in similar response of riparian habitats in comparison to allotments not grazed for 10 years. However, controlled grazing strategies require more intensive management, such as use of smaller fenced riparian pastures and herding to improve livestock distribution and rotation, and adaptively variable timing of rest and grazing (Kovalchik & Elmore 1992; Freitas et al. 2014; Swanson et al. 2015). Furthermore, it remains largely unknown to what extent controlled grazing can reverse already degraded conditions over the long term, especially given that restoration of willows may lag behind other species even with exclusion (Hough-Snee et al. 2013). For streams that are highly degraded or incised, restoration also may require planting and protecting willows, in conjunction with other techniques to restore more natural hydrologies and floodplains, such as the use of beaver dam analogs and other instream structures (Dreesen et al. 2001; Hall et al. 2011; Hough-Snee et al. 2013; Pollock et al. 2015). Until livestock grazing is managed in a way that produces adequate amounts of willow growth, the restoration of dam-building beaver is not likely to be possible in many areas.

Acknowledgments

This study was supported by the USDA NIFA Hispanic Serving Institutions grant no. 2011-38422-30947 awarded to Dr. M. Desmond; we owe her special thanks. We thank I. Barela for assistance with data collection and F. Cortez, P. Garcia, S. Ramakrishnan, J. Stuart, C. Wild, B. Bird, C. Creech, L. Lucero, G. Long, G. Holm, T. Medina, D. Gurule, D. Blagg, S. Franklet, R. Paynter, W. Sauter, K. Menke, L. Knutson, and J. Martinez for accesses to sites and logistical support. We greatly appreciate R. Goljani for GIS and computer assistance, T. C. Frey for helpful comments, N. T. Quintana for information about elk densities, and staff of Carson National Forest, including F. Cortez, J. Gatlin, M. Herrera, and A. Radcliff, for information on livestock grazing. We thank B. Baker, J. W. Cain, M. J. Desmond, I. Perkins-Taylor, two anonymous reviewers, and the editors for helpful comments on a previous version of this article. This study was conducted in partial completion of a Master's degree by BAS. The authors have no conflicts of interest to declare.

LITERATURE CITED

Albert S, Trimble T (2000) Beavers are partners in riparian restoration on the Zuni Indian reservation. Ecological Restoration 18:87–92

Aleksiuk M (1968) Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759–762

Allen AW (1983) Habitat suitability index models: Beaver. FWS/OBS82/10.30 revised, U.S. Fish and Wildlife Service, Washington, D.C.

Allison PD (1999) Logistic regression using the SAS system: theory and application. SAS Institute Inc., Cary, North Carolina

Andersen DC, Shafroth PB, Pritekel CM, O'Neill MW (2011) Managed flood effects on beaver pond habitat in a desert riverine ecosystem Bill Williams River, Arizona U.S.A. Wetlands 31:195–206

Apple LL, Smith BH, Dunder JD, Baker BW (1985) The use of beavers for riparian/aquatic habitat restoration of cold desert, gully-cut stream systems in southwestern Wyoming. Pages 123–130. In: Pilleri G (ed) Investigations on beavers. Vol IV. Brain Anatomy Institute, Berne, Switzerland

Bailey V (1931) Mammals of New Mexico. North American Fauna 53:1–412

Baker BW, Hill EP (2003) Beaver (*Castor canadensis*). Pages 288–310. In: Feldhamer GA, Thompson BC, Chapman JA (eds) Wild mammals of North America: biology, management, and conservation. 2nd edition. The John Hopkins University Press, Baltimore, Maryland

Baker BW, Ducharme HC, Mitchell DCS, Stanley TR, Peinetti HR (2005) Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications 15:110–118

Barnes DM, Mallik AU (1996) Use of woody plants in construction of beaver dams in northern Ontario. Canadian Journal of Zoology 74:1781–1786

Baker BW, Peinetti HR, Coughenour MB, Johnson TL (2012) Competition favors elk over beaver in a riparian willow ecosystem. Ecosphere 3:1–15

Barnes DM, Mallik AU (1997) Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management 61:1371–1377

Batchelor JL, Ripple WJ, Wilson TM, Painter LE (2014) Restoration of riparian areas following the removal of cattle in the northwestern Great Basin. Environmental Management 55:930–942

Beier P, Barrett RH (1987) Beaver habitat use and impact in Ruckee River basin, California. Journal of Wildlife Management 51:794–799

Belsky JA, Matzke A, Uselman S (1999) Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431

Bird B, O'Brien M, Petersen M (2011) Beaver and climate change adaptation in North America. http://www.wildearthguardians.org/site/DocServer/Beaver_and_Climate_Change_Final.pdf?docID=3482 (accessed 1 Dec 2015)

Booth DT, Cox SE, Simonds G, Sant ED (2012) Willow cover as a stream-recovery indicator under a conservation grazing plan. Ecological Indicators 18:512–519

Bowling GA (1941) The introduction of cattle into colonial North America. Journal of Dairy Science 25:129–154

Brookshire EN, Kauffman JB, Lytjen D, Otting N (2002) Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia 132:559–566

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York

Bursac Z, Gauss CH, Williams DK, Hosmer DW (2008) Purposeful selection of variables in logistic regression. Source Code for Biology and Medicine 3:17, DOI: 10.1186/1751-0473-3-17

Carrillo C, Bergman D, Taylor J, Nolte D, Viehoever P, Disney M (2009) An overview of historical beaver management in Arizona. USDA National Wildlife Research Center, Fort Collins, Colorado, Staff Publications, Paper No. 882

Case RL, Kauffman JB (1997) Wild ungulate influence on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. Northwest Science 71:115–126

Clary WP (1999) Stream channel and vegetation responses to late spring cattle grazing. Journal of Range Management 52:218–227

Daubenmire R (1959) A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64

Dominguez F, Rivera E, Lettenmaier DP, Castro CL (2012) Changes in winter precipitation extremes for the western United States under warmer climate as simulated by regional climate models. Geophysical Research Letters 39:L05803

Doucet CM, Adams IT, Fryxell JM (1994) Beaver dam and cache composition: are woody species used differently? Ecoscience 1:268–270

Dreesen D, Harrington J, Subirge T, Stewart P, Fenchel G (2001) Riparian restoration in the Southwest: species selection, propagation planting methods, and case studies. Pages 253–272. National Nursery Proceedings—1999, 2000, 2001. Proceedings RMRS-P-24. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado

Findley JS, Harris AH, Wilson DE, Jones C (1975) Mammals of New Mexico. University of New Mexico Press, Albuquerque

Fouty S (2003) Current and historic stream channel response to changes in cattle and elk grazing pressure and beaver activity. PhD dissertation. Department of Geography, University of Oregon, Eugene

Freitas MR, Roche LM, Weixelman D, Tate KW (2014) Montane meadow plant community response to livestock grazing. Environmental Management 54:301–308 DOI: 10.1007/s00267-014-0294-y

Fryxell JM, Doucet CM (1993) Diet choice and the functional response of beavers. Ecology 74:1297–1306

Gallant D, Berube CH, Tremblay E, Vasseur L (2004) An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality. Canadian Journal of Zoology 82:922–933

Greenland S (1989) Modeling and variable selection in epidemiologic analysis. American Journal of Public Health 79:340–349

Gurnell AM (1998) The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22:167–189

Hall J, Pollock M, Hoh S (2011) Methods for successful establishment of cottonwood and willow along an incised stream in semiarid eastern Oregon, U.S.A. Ecological Restoration 29:261–269

Holecheck JL, Galt D (2000) Grazing intensity guidelines. Rangelands 22:11–14

Holland KA, Leininger WC, Trlica MJ (2005) Grazing history affects willow communities in a montane riparian ecosystem. Rangeland Ecology & Management 58:148–154

Hood GA, Bayley SE (2008a) Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biological Conservation 141:556–567

Hood GA, Bayley SE (2008b) The effects of high ungulate densities on foraging choices by beaver (*Castor canadensis*) in the mixed-wood boreal forest. Canadian Journal of Zoology 86:484–496

Hough-Snee N, Roper BB, Wheaton JM, Budy P, Lokteff RL (2013) Riparian vegetation communities change rapidly following passive restoration at a northern Utah stream. Ecological Engineering 58:371–377

Howard RJ, Larson JS (1985) A stream habitat classification system for beaver. Journal of Wildlife Management 49:19–25

Huey WS (1956) New Mexico beaver management plan. New Mexico Department of Game and Fish, Santa Fe

Jenkins SH (1975) Food selection by beavers. Oecologia 21:157–173

Jenkins SH (1979) Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112–116

Jenkins KJ, Manly BFJ (2008) A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. Journal of Applied Ecology 45:1339–1348

Kauffman JB, Krueger WC, Vavra M (1983) Effects of late season cattle grazing on riparian plant communities. Journal of Range Management 36:685–691

Keller TM (2014) Senate Memorial 4: recognizing the watershed health benefits of North American beaver populations; Requesting recommendations for a statewide beaver management plan. State of New Mexico Senate Proceedings, Santa Fe

Kindschy RR (1989) Regrowth of willow following simulated beaver cutting. Wildlife Society Bulletin 17:290–294

Kovalchik BL, Elmore W (1992) Effects of cattle grazing systems on willow-dominated plant associations in central Oregon. Pages 111–119. In: Clary WP, McArthur ED, Bedunah D, Wambolt CL (eds) Proceedings-symposium on ecology and management of riparian shrub communities General Technical Report INT-289. USDA Forest Service

Lancia RA, Kendall WL, Pollock KH, Nichols JD (2005) Estimating the number of animals in wildlife populations. Pages 106–154. In: Braun CE (ed) Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland

Love CM (1916) History of the cattle industry in the southwest. The Southwestern Historical Quarterly 19:370–399

Lucas RW, Baker TT, Wood MK, Allison CD, Vanleeuwen DM (2004) Riparian vegetation response to different intensities and seasons of grazing. Journal of Range Management 57:466–474

Macfarlane WW, Wheaton JM, Bouwes N, Jensen ML, Gilbert JT, Hough-Snee N, Shivik JA (In Press) Modeling the capacity of riverscapes to support beaver dams. Geomorphology, DOI: 10.1016/j.geomorph.2015.11.019

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Norwell, Massachusetts

McComb WC, Sedell JR, Buchholz TD (1990) Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273–281

Müller-Schwarze D, Sun L (2003) The Beaver: natural history of a wetlands engineer. Comstock Publishing Associates, Ithaca, New York

Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212

Ohmart RD, Anderson BW (1986) Riparian Habitats. Pages 169–199. In: Cooperrider AY, Boyd RJ, Stuart HR (eds) Inventory and monitoring of wildlife habitat. USDI, Bureau of Land Management, Denver, Colorado

Patten DT (1998) Riparian ecosystems of semi-arid North America: diversity and human impacts. Wetlands 18:498–512

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11:1633–1644

Peinetti HR, Baker BW, Coughenour MB (2009) Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. Ecological Modelling 220:998–1012

Pelster AJ, Evans S, Leininger WC, Trlica MJ, Clary WP (2004) Steer diets in a montane riparian community. Journal of Range Management 57:546–552

Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C (2014) Using beaver dams to restore incised stream ecosystems. Bioscience 64:279–290

Pollock MM, Pess GR, Beechie TJ (2004) The importance of beaver ponds to Coho salmon production in the Stillaguamish River basin, Washington, U.S.A. North American Journal of Fisheries Management 24:749–760

Pollock MM, Lewallen G, Woodruff K, Jordan CE, Castro JM (2015) The beaver restoration guidebook: working with beaver to restore streams, wetlands, and floodplains. Version 1.0. United States Fish and

Wildlife Service, Portland, Oregon. http://www.fws.gov/oregonfwo/ToolsForLandowners/RiverScience/Beaver.asp (accessed 1 Dec 2015)
Rickard WH, Cushing CE (1982) Recovery of streamside woody vegetation after exclusion of livestock grazing. Journal of Range Management 35:360–361
Ripple WJ, Beschta RL (2012) Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation 145:205–213
Robel RJ, Biggs JN, Dayton AD, Hulbert LC (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297
Rosell F, Bozser O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35:248–276
Rosner B (2000) Fundamentals of biostatistics. Duxbury, Pacific Grove, California
Schulz TT, Leininger WC (1990) Differences in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43:295–299
Seager R, Ting MF, Held I, Kushnir Y, Lu J, Vecchi G, et al. (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184
Singer FJ, Mark LC, Cates RC (1994) Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443
Slough BG, Sadleir RMFS (1977) A land capability classification system for beaver (*Castor canadensis* Kuhl). Canadian Journal of Zoology 55:1324–1335
Stoffyn-Egli P, Willison JHM (2011) Including wildlife habitat in the definition of riparian areas: the beaver (*Castor canadensis*) as an umbrella species for riparian obligate animals. Environmental Reviews 19:479–494
Stromberg JC, McCluney KE, Dixon MD, Meixner T (2013) Dryland riparian ecosystems in the American Southwest: Sensitivity and resilience to climatic extremes. Ecosystems 16:411–415
Suzuki N, McComb WC (1988) Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon coast range. Northwest Science 72:102–110
Svendsen GE (1980) Seasonal change in feeding patterns of beaver in southeastern Ohio. Journal of Wildlife Management 44:285–290
Swanson S, Wyman S, Evans C (2015) Practical grazing management to maintain or restore riparian functions and values on rangelands. Journal of Rangeland Applications 2:1–28
Weber DJ (1971) The Taos trappers: the fur trade in the far Southwest, 1540–1846. University of Oklahoma Press, Norman
Wild C (2011) Beaver as a climate change adaptation tool: concepts and priority sites in New Mexico. Seventh Generation Institute, Santa Fe, New Mexico. http://static1.squarespace.com/static/54c6efebe4b05d1a1cc71a3f/t/54d3a9c4e4b04682afea3b39/1423157700638/Beaver+As+a+Climate+Change+Adaptation+Tool+–+Concepts+and+Priority+Sites+in+New+Mexico.pdf (accessed 1 Dec 2015)
WildEarth Guardians (2013) Assessing beaver habitat on federal lands in New Mexico. Contract #13-667-5000-0007. Final report 31 July 2013. https://www.env.nm.gov/swqb/Wetlands/projects/Beavers/FinalReport07-31-2014.pdf (accessed 1 Dec 2015)

Supporting Information

The following information may be found in the online version of this article:

Table S1. Data on variables at sites with an active beaver dam present ($n = 29$) or absent ($n = 28$).
Table S2. Data on variables at sites with different livestock grazing policy.
Table S3. Evaluation of grazing policy as a confounder on the relationship between vegetation variables and the presence or absence of an active beaver dam.
Figure S1. Locations of active primary dams created by the American beaver (*Castor canadensis*) on public lands in New Mexico during 2013 (green circles).

Coordinating Editor: James Anderson

Received: 10 August, 2015; First decision: 22 September, 2015; Revised: 5 March, 2016; Accepted: 6 March, 2016; First published online: 11 May, 2016

Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Ecosystem services provided by beavers *Castor* spp.

Stella THOMPSON* *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: stella.thompson@helsinki.fi*
Mia VEHKAOJA *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: mia.vehkaoja@helsinki.fi*
Jani PELLIKKA *Natural Resources Institute Finland, Latokartanonkaari 9, 00790, Helsinki, Finland. Email: jani.pellikka@luke.fi*
Petri NUMMI *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: petri.nummi@helsinki.fi*

Keywords
ecosystem services, Eurasian beaver *Castor fiber*, meta-analytical function transfer, monetary valuation, North American beaver *Castor canadensis*, Northern Hemisphere, payments for ecosystem services

*Correspondence author

Received: 29 May 2018
Accepted: 26 May 2020
Editor: DR

doi: 10.1111/mam.12220

ABSTRACT

1. We aimed to recognise beaver-produced ecosystem services and quantify their theoretical value for the entire Northern Hemisphere. Activity of the Eurasian beaver *Castor fiber* and the North American beaver *Castor canadensis* in the landscape provides ecosystem services and disservices. Services produced by beaver activity include water purification, moderation of extreme events, habitat and biodiversity provision, nutrient cycling, greenhouse gas sequestration, recreational hunting and fishing, water supply, and non-consumptive recreation. Beaver-produced services have not been compiled, analysed, or quantified previously.
2. Each service we evaluated is worth millions to hundreds of millions of US dollars (USD) annually. Habitat and biodiversity provision (133 million USD), along with greenhouse gas sequestration (75 million USD), are particularly valuable services in absolute terms, while non-consumptive recreation (167 USD ha^{-1}) and habitat and biodiversity provision (133 USD ha^{-1}) have the largest annual per-hectare values.
3. Our results can be used to broaden decision-making and management perspectives, as we offer value estimates to wildlife managers and municipality planners for assessing local site-specific beaver wetland values and the opportunities for their realisation. Implementing Payments for Ecosystem Services schemes offer a concrete way for societies to benefit from beaver-produced services while concurrently compensating beaver-produced losses accrued to landowners. Building such schemes offer long-term realisation of ecosystem services and damage mitigation. This would lead to increased societal well-being and increased conservation interest and efforts.

INTRODUCTION

Various ecosystem functions and products, such as clean air, water, and food, are conditions and processes necessary or beneficial to humans (Millennium Ecosystem Assessment 2005a) and are referred to as ecosystem services. Ecosystem services directly or indirectly sustain humans, as they are necessary for the functioning of societies and for the ability of ecosystems to absorb unwanted by-products of economic production (Boyd & Banzhaf 2007). Ecosystem services are environmental assets that may be actively or passively gained, consumed, used, and enjoyed. The MEA divides the services into four categories according to their functions and benefits: regulating, provisioning, supporting, and cultural (MEA 2005a).

Many environmental assets are currently being depleted and degraded at rates more rapid than their renewal. As several environmental assets are crucial to the balanced functioning of societies, their conservation has become a priority. However, as long as ecosystem services remain

outside of economic markets, no fiscal incentives are in place for their conservation (Farley & Costanza 2010). This has created a need for their monetary valuation, to aid policy- and decision-makers. Economic valuation using commensurate monetary or other measures is necessary for decision-makers assessing the effects of various ecosystem services and the outcomes of their utilisation (Liu et al. 2010). Once valuation is complete, preservation of the produced benefits is next on the agenda. Several mechanisms exist for this, such as Payment for Ecosystem Services schemes (Ezzine-de-Blas et al. 2016), in which economic processes are used to incentivise resource managers (e.g. landowners) to uphold an existing ecosystem service on their land in return for monetary benefits from a beneficiary (e.g. a nearby community or industrial factory). The schemes compensate for conservation-related losses accrued to resource managers. Currently, schemes for wetlands or water management are in place for, e.g. carbon storage, storm-water management, nutrient recycling, and water filtration in, e.g. France, the USA (Oregon), and the UK (e.g. Guillozet 2015). Beaver (*Castor* spp.) wetlands provide all of these services, but so far no Payment for Ecosystem Services schemes have been implemented in these areas.

Beavers and their ecosystem engineering are natural components of freshwater wetlands in the Northern Hemisphere (Johnston 2017). These wetlands have co-evolved along with the species. Beavers modify their surroundings and influence succession, potentially leading to novel ecosystems, such as beaver wetlands and beaver meadows, with unique habitat characteristics. Beaver occupancy forms new habitats (Whitfield et al. 2015), as beavers strongly affect the structures and functions of ecosystems and concurrently provide ecosystem services for humans through their habitat modification. Increasing beaver populations may also increase the future value of the services they provide. The Eurasian beaver *Castor fiber* and the North American beaver *Castor canadensis*, both included in this review, are classified as Least Concern according to the International Union for Conservation of Nature.

Much is known of the physical and ecological alteration that beaver activity causes, and beaver activity has been studied extensively from an ecological perspective. However, we aim to take a utilitarian viewpoint and assess beaver ecosystem engineering through the human-centred ecosystem services approach that focuses solely on the benefits of nature for humans. This allows us to look at how societies may benefit from or endure beaver activity. No previous quantification has been performed for the magnitude and value of the effects of beavers and how they directly or indirectly reflect onto individual stakeholders or societies. From an ecological perspective, beavers do not damage or negatively influence their surroundings (except for in areas in the Southern Hemisphere where the North American beaver is invasive), but from an ecosystem services viewpoint, damage (i.e. disservices) to humans does occur. In our assessment, many of these effects appear as disservices at the stakeholder level (e.g. beaver-induced flooding of forests) while simultaneously emerging as services to society at large (e.g. upholding water supplies; Bhat et al. 1993, Siemer et al. 2013). The ecosystem services approach is limited, as it does not consider how humans in turn have degraded and narrowed the behaviour and function of organisms in their natural habitats.

We formulate direct and indirect impact chains of beaver action leading to human well-being using existing data. We use the ecosystem services frame to identify the key chains producing the services; these impact chains are relevant focal points for future management options. We do this by quantifying preliminary estimates of current Northern Hemisphere freshwater mineral soil wetland and beaver values. Data valuing disservices are scarce and dated, and we therefore concentrate solely on describing and quantifying the services that are provided by beavers. Our aim with this utilitarian focus is to broaden current decision-making and management perspectives, which could aid in regulating and utilising beaver activity to help maximise societal well-being and lead to increased conservation efforts and further research. We approach this aim by producing estimates based on values found in the literature, to achieve a first and theoretical attempt at valuing ecosystem services provided by beavers.

METHODS

As our study relates to beaver wetlands, we first gained insight into global wetland resources and their valuation (e.g. Schuyt & Brander 2004, Ramsar Convention on Wetlands 2018). The value of wetlands has long been debated, and they are currently valued for a multitude of reasons and needs (MEA 2005a). Foremost, it is important to understand how to maximise the benefits and turnarounds gained from wetland habitats, while upholding a trade-off or balance between these gained values and conservation actions conducted and/or damages incurred (Gustavson & Kennedy 2010).

We used the ecosystem services categorisations for wetlands in Haines-Young and Potschin (2018), MEA (2005b) and Russi et al. (2013) to determine which services beavers provide in the Northern Hemisphere (Table 1 and Fig. 1). Service-specific valuation was required to gain an idea of how valuable individual ecosystems are to societies. Valuation methods aim to bridge economic and environmental accounting, making the monetary valuation of ecosystem services, and thereby decision-making concerning them, more straightforward.

Table 1. Ecosystem services provided by beavers in the Northern Hemisphere and their categories, along with the number of approved value estimates found for each service during the database and literature searches; this number of value estimates was used in the meta-analytical function transfer. The abbreviated name of each variable as used in meta-analytical function transfer is indicated in parentheses

Ecosystem service	Ecosystem service category	Number of value estimates
Moderation of extreme events (FloodDrought)	Regulating	11
Greenhouse gas sequestration (GHG)	Regulating	8
Water purification (Quality)	Regulating	26
Water supply (Supply)	Provisioning	6
Recreational hunting and fishing (HuntFish)	Provisioning	3
Habitat and biodiversity provision (HabBio)	Supporting	8
Nutrient cycling*	Supporting	0
Non-consumptive recreation (Recreation)	Cultural	17
Historical value*	Cultural	0

*Our search provided no service value, so this ecosystem service was left out of our analyses.

Database search and literature review

We searched for relevant literature in seven ecosystem valuation databases (Appendix S1) and found relevant studies in two: the Environmental Valuation Reference Inventory database and The Economics of Ecosystems and Biodiversity – Valuation Database. We used ResearchGate and Web of Science to search for additional relevant literature using the word "beaver" combined with terms such as "ecosystem services", "flooding", "carbon balance", "methane", "mercury", "nutrients", "biodiversity", "water", and the word "wetlands" coupled with "value", "valuation", and "ecosystem services". The following inclusion criteria were applied to the documents found in all searches: all documents (1) concerned freshwater mineral soil wetlands in the Northern Hemisphere, (2) only incorporated specific wetland ecosystem services, (3) involved primary research, to avoid double counting, and (4) were published between 2000 and 2018. The database search was conducted between 15 and 18 October 2018. Our literature search only incorporated general freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of the Northern Hemisphere beaver range, because we wished to ensure that our results would not be overestimated due to value estimates from ecosystems and climates outside of the beaver range.

We examined the whole documents to ensure they contained all relevant information needed for our analysis, i.e. information on currency year, type of valuation method, size of the study area, and study and area population when applicable (i.e. for willingness-to-pay studies). If a

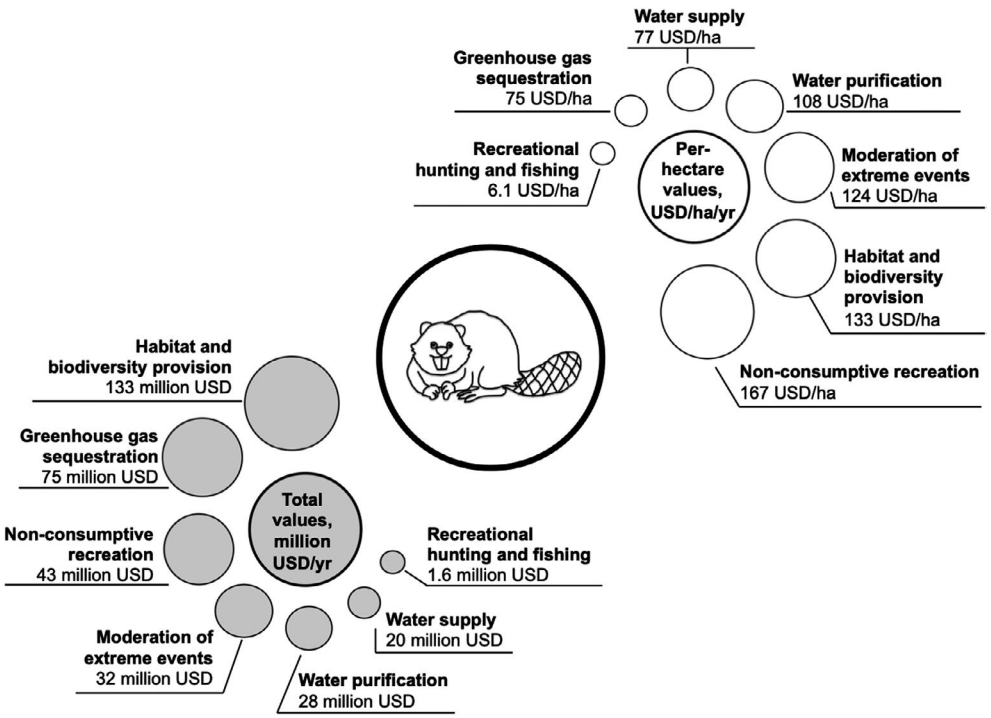


Fig. 1. Values of ecosystem services produced by beaver ponds, given in annual per-hectare values (white circles) and aggregated over the one million ha Northern Hemisphere beaver range per year (grey circles). Circles are not to scale.

study did not specify the exact surface area but defined an exact location (e.g. an entire country or a specific county or municipality), we searched online for information on surface area. All documents we accepted were written in English. We included estimates from the documents using contingent valuation, choice experiment, travel, replacement or avoidance cost, or market price methods, and all values were converted into annual values per hectare.

Beaver population and beaver wetland area

We examined the Northern Hemisphere, covering boreal, temperate forest, temperate grassland, and chaparral regions in North America and Eurasia (Europe and Russia). We used beaver range maps in Touihri et al. (2018) and Halley et al. (2012) to narrow our search and analyses to cover only the current approximate combined geographic range of both beaver species, which was located between 69°N and 26°N. North American beaver populations appear to be stable, so we used the lower bound estimates for population (9.6 million), colony number (2.4 million colonies) and pond area (928900 ha) for North America, as reported by Whitfield et al. (2015). The beaver populations in several countries of Eurasia are increasing, so we used the population estimate (1.5 million individuals) in Halley et al. (2021). The combined North American and Eurasian estimates raised the total Northern Hemisphere population to 11.1 million individuals. Colony numbers and pond area estimates for Eurasia were calculated using the 1.5 million individual population estimate to recalculate the Eurasian values in Whitfield et al. (2015). They incorporated differences in pond-building frequencies and dam numbers between the two beaver species, which is why we felt comfortable basing our estimates on the study. However, the pond area estimate in Whitfield et al. (2015) only included dam-building beavers. Beavers inhabit varying habitats from riverine to open water areas, and the degree to which they build dams and create ponds varies due to habitat characteristics. The percentage of beavers that build dams has been studied in several countries. Some studies show a similar percentage for both species (e.g. Danilov & Fyodorov 2015: Eurasian 74% vs. North American 77%), while others suggest that Eurasian beavers dam less frequently (e.g. Zav'yalov 2011: Eurasian beaver 10–63%; Whitfield et al. 2015: North American beaver 50–80%). Our valuations focus on dam-building beavers, which, according to these estimates, make up 49–69% of the beaver population. We are aware that the services provided in various beaver habitats may differ to some extent from each other. Also, individual beavers are not strictly dam-builders or non-dam-builders, but rather build dams depending on the situation. However, damming does appear to be common in both species. We have compiled our calculations assuming that half of the Northern Hemisphere beaver population builds dams at any given time.

Meta-analytical function transfer of beaver wetland values

We performed a meta-analytical function transfer, where wetland values from primary valuation studies were compared against "various covariates relating to policy site characteristics and research design choices made by authors" (Chaikumbung & Scarborough 2016). As the method utilises values from several previous studies and study sites, a greater variety of ecosystems and site conditions may be incorporated into the calculations (Brander 2006), which potentially increases the validity estimated over large geographic areas. We transferred the values from the ecosystem services valuation studies we collected, using the meta-analytic regression model given in Equation 1.

$$\ln y_{ij} = \gamma ES_{ij} + \beta^b X^b_{ij} + \beta^s X^s_{ij}, s \quad (1)$$

where y_{ij} was the monetary value of a wetland in US dollars (USD) per hectare per year, *ES* included the ecosystem services provided by a beaver wetland, X^b was a vector describing wetland type, and X^s was a vector describing the study characteristics (i.e. survey method). Subscript i was the number of studies ($i = 1 \ldots 44$), and subscript j is the number of observations ($j = 1 \ldots 75$). Vectors β^b, β^s, and γ contained coefficients to be estimated for the explanatory variables X^b, X^s, and *ES*, respectively. We used ordinary least squares regression for the estimation. The dependent variable was the natural logarithm transformation of the annual per-hectare USD value for each wetland.

First, we standardised price values from various countries and years into comparable values. To do this, we used purchasing power parity adjusted exchange rates to convert the various currencies from our valuation study sites into USD at 2017 price levels. This controlled for differences in price levels between countries. To adjust prices to account for inflation, we used gross domestic product inflators from the World Bank (2018) as in Brander (2006). We then calculated their relative values as the real value of each service.

These values were next used in the function transfer. The resulting coefficients for ɣ indicated the "direction and magnitude of the effect of each explanatory variable on the unit value of wetland ecosystem services" (Brander 2006). We then calculated the exponentials for the coefficients, i.e. annual per-hectare values for each service, and combined them with the beaver wetland area estimate

we had calculated. This formed an aggregated magnitude estimate of individual ecosystem services provided by beavers for the entire Northern Hemisphere. Most wetland meta-analyses have included wetlands from around the world, while ours only incorporated wetlands in beaver habitats in the Northern Hemisphere. With this, we hoped to avoid overestimations in ecosystem service values that could be caused by differences in Northern and Southern Hemisphere wetlands.

Geographic information system analysis

Ecosystem services relate to human demand and need; a service remains only potential until a society requires or covets it, at which point the potential service becomes real (Grunewald & Bastian 2015). No studies have assessed the required proximity of beaver wetlands to human habitation in relation to ecosystem services, and conducting a thorough analysis of geographic proximity to determine this was beyond the scope of our study. However, to avoid completely disregarding this aspect, we roughly analysed the percentage of beaver wetland area coinciding with three human population density classes (sparse population: 1–199 people per km^2; moderate population: 200–999 people per km^2; dense population: 1000+ people per km^2). The resulting percentages were then used as human population density coefficients in our calculations (hereafter termed 'density coefficient'). The value of locally functioning ecosystem services was calculated using only the percentage of beaver wetland area where human habitation was dense or moderate; i.e., the percentage of sparse human habitation was left out of the calculations. The areas of the intersecting polygons for calculating the coefficients were computed using QGIS 2.18. The global land cover map (ESA GlobCover 2009) was used for the wetland data, and the 2015 data from the Gridded Population of the World, v4.10 (Center for International Earth Science Information Network 2017) were used for the human population data.

RESULTS

Our database search produced 105 documents fulfilling the four inclusion criteria (see 'Database search and literature review' above). After examining each of these documents for relevant information, we ended up with 43 utilisable documents (articles, grey literature texts, reports, books); 75 individual value observations were obtained from these documents. Studies and reports were found from 14 countries. Sixty-three per cent (27 texts) of the documents were from Europe, 37% (16 texts) from North America, and none from Russia. Studies were spread across four biomes: temperate forest (23 texts, 52%), boreal forest (9 texts, 20%), temperate grassland (6 texts, 14%), and chaparral (4 texts, 9%), while 5% (two texts) spread over both the boreal and temperate forest zones. The studies identified the study habitat as lacustrine (14%), riverine (18%), or urban (9%) wetlands, while a majority (61%) of the studies either incorporated several wetland types or did not specify the habitat. These we clumped together as general freshwater wetlands. A list of the documents used in our final beaver wetland valuation can be found in Appendix S2. The most common reason for discarding a document was that it did not provide information on the currency year a study used, so that we were unable to calculate purchase power parities for the values provided. We did not find utilisable value estimates filling all our inclusion criteria for nutrient cycling or historical value (a 'cultural' service), so our final meta-analytical function transfer included values for the following ecosystem service variables (see Table 1): moderation of extreme events (variable FloodDrought), greenhouse gas sequestration (GHG), water purification (Quality; all services in the 'regulating' category), water supply (Supply), recreational hunting and fishing (HuntFish; both 'provisioning' services), habitat and biodiversity provision (HabBio; a 'supporting' service), and non-consumptive recreation (Recreation; a 'cultural' service).

Northern Hemisphere beaver wetland resources, meta-analytical function transfer, and geographic information system analysis

The total beaver population is increasing in the Northern Hemisphere (Gibson & Olden 2014, Whitfield et al. 2015, Halley et al. 2021). Current Northern Hemisphere population estimates and dam-building beaver wetland area estimates are shown in Table 2. We used these values as the basis for calculating all other estimates in our study, and the area estimate was also used for scaling up our meta-analytical function transfer results. Table 3 presents the mean and standard deviations for the ecosystem service values, and Table 4 presents the results of our meta-analytical value transfer.

None of the ecosystem services differed significantly from the others; i.e., none of the services was valued exceptionally high or low in the meta-regression, probably because we only included Northern Hemisphere studies that were located between the northern and southern latitude limits of the beaver range (69°N and 26°N). For example, habitat and biodiversity provision and recreational hunting and fishing services may be valued more highly in the tropics, which are not included

Table 2. Beaver population and colony estimates, and estimates for beaver pond area in the Northern Hemisphere. Estimates were calculated by extrapolating data from Whitfield et al. (2015) and Halley et al. (2021)

	Europe and Russia	North America	Total Northern Hemisphere
Beaver population	1.5 million	9.6 million	11.1 million
Total number of beaver colonies	242000–405000	1.5–2.6 million	1.8–3.0 million
Number of dam-building colonies			895000–1.5 million
Beaver pond area, ha	24600–181000	928900	952600–1109000*

*Rounded to 1 million ha in our calculations.

Table 3. Definition and description of the dependent variable and explanatory variables used in the meta-regression model. Mean values for each variable indicate the mean value per hectare per year given in US dollars standardised to the year 2017. For the dependent variable, the mean is given as the natural logarithm

	Variable	Mean	Standard deviation
Dependent variable	Wetland value, USD(2017) ha^{-1} yr^{-1} (ln)	7.152	8.263
Wetland variables			
Ecosystem services	Greenhouse gas sequestration (GHG)	1.462	0.891
	Moderation of extreme events (FloodDrought)	1.973	0.827
	Water supply (Supply)	1.160	1.099
	Water purification (Quality)	1.795	1.426
	Habitat and biodiversity provision (HabBio)	1.882	1.012
	Recreational hunting and fishing (HuntFish)	1.811	1.273
	Non-consumptive recreation (Recreation)	2.137	1.091
Wetland type	General freshwater wetland	1.609	1.121
	Lacustrine wetland	1.833	0.581
	Riverine wetland	2.466	1.513
	Urban wetland	2.880	0.155
Study variables			
Valuation method	Contingent valuation	1.374	1.258
	Choice experiment	2.474	0.887
	Travel cost method	1.561	0.862
	Avoidance cost	2.175	0.921
	Replacement cost	3.797	0.544
	Market prices	1.666	0.660

in our dataset. This may lead to aggregation bias in our data, where the mean values of individual variables are similar between different studies (Borenstein et al. 2009, Deeks et al. 2019). While substantial variation may occur within a study, the meta-regression uses study-level means to summarise data, and therefore, relationships between an explanatory variable (i.e. meta-regression variable) and the outcome variable may not become apparent. Predefined study weighting in the meta-regression also causes larger studies to have more pronounced effects on the coefficients (Deeks et al. 2019). Coefficient significance shows a linear relationship between the explanatory and outcome variables. The model is semi-logarithmic, so the correct annual per-hectare values for individual services are calculated by taking the exponentials of the related meta-regression coefficients in Table 4.

We used contingent valuation as a reference method in the meta-regression and obtained significant results for four (contingent valuation, travel cost, replacement cost, and market price methods) of the six valuation methods assessed in the model. Other meta-analyses have previously determined significant differences for three valuation methods (replacement cost: Woodward & Wui 2001; contingent valuation: Brander 2006; travel cost method: Reynaud & Lanzanova 2017), so our results are in line with previous studies. We also assessed the importance of habitat on the valuation results and found that general freshwater habitats produced significantly lower values and urban wetlands produced significantly higher values than the other habitats. Urban wetlands may be valued more highly because they provide nature values in areas with little natural habitat. General freshwater habitats may be significant because most of the studies (61%) in our meta-regression are grouped into this category, and model weighting may cause larger groups to have a stronger effect on the outcome.

Table 4. Estimates of the meta-regression models with random effects. Ordinary least squares results were as follows: adjusted R^2 = 0.231. N = 75. Statistical significance is indicated with ***, **, and * for 1, 5, and 10% levels, respectively

	Variable	Coefficient	p-value
Wetland variables			
Ecosystem services	Greenhouse gas sequestration (GHG)	4.314	0.816
	Moderation of extreme events (FloodDrought)	4.817	0.661
	Water supply (Supply)	4.342	0.844
	Water purification (Quality)	4.680	0.792
	Habitat and biodiversity (HabBio)	4.887	0.616
	Recreational hunting and fishing (HuntFish)	1.811	0.839
	Non-consumptive recreation (Recreation)	5.119	0.374
Wetland type	General freshwater wetland	3.085**	0.034
	Lacustrine wetland	3.632	0.251
	Riverine wetland	3.516	0.180
	Urban wetland	2.880*	0.069
Study variables			
Valuation method	Contingent valuation	2.284***	0.001
	Choice experiment	3.390	0.146
	Travel cost method	2.459**	0.012
	Avoidance cost	3.406	0.144
	Replacement cost	3.796**	0.011
	Market prices	2.886**	0.044

We determined greenhouse gas sequestration (variable GHG) and habitat and biodiversity provision (HabBio) to function at global scales; i.e., their monetary realisation was not strongly or directly influenced by human population density and their human density coefficients are therefore equal to one. On the other hand, moderation of extreme events (FloodDrought), water supply (Supply), water purification (Quality), recreational hunting and fishing (HuntFish), and non-consumptive recreation (Recreation) services function at local scales and are dependent on sufficient human population densities for their utilisation to be feasible. The density coefficient for moderate and dense human population density derived from our geographic information system analysis was 0.26, which was used as the density coefficient for local-level services. Figure 1 and Table 5 show the annual per-hectare values and quantified values of beaver activity over one million ha of beaver ponds in the Northern Hemisphere. The value results in Table 5, and those presented hereafter, relate to the approximately 50% of beavers that build dams. Non-consumptive recreation, habitat and biodiversity provision, and moderation of extreme events had the highest annual per-hectare values (167, 133, and 124 USD(2017) per ha per year), while recreational hunting and fishing was valued the lowest (6.1 USD(2017) per ha per year). However, when combined with the density coefficients, habitat and biodiversity provision, greenhouse gas sequestration, and non-consumptive recreation became the most valuable ecosystem services over the one million ha Northern Hemisphere beaver area.

Regulating services provided by beavers

Moderation of extreme events

Beaver-created wetlands modify natural flow regimes by increasing surface- and groundwater retention, thereby moderating extreme events. Flood peaks are mitigated through rainwater retention and drought conditions by slowly releasing water through dams (Rosell et al. 2005, Westbrook et al. 2006, Burchsted et al. 2010, Gibson & Olden 2014). A single beaver dam may modify the volume of flowing water by 3400–628000 m^3 per annum, depending on ecosystem and water system characteristics (Buckley et al. 2011). Calculating using the lower bound value (3400 m^3) equates to all Northern Hemisphere

Table 5. Annual per-hectare service values and aggregated economic value of beaver wetland ecosystem services in the Northern Hemisphere, calculated using our meta-regression value function, and the density coefficient used to aggregate per-hectare values. Meta-regression variable names are given in parentheses

Ecosystem service	Per-hectare service value USD(2017) ha^{-1} yr^{-1}	Value of ponds created by dam-building beavers (1 million ha) USD(2017) yr^{-1}	Density coefficient used in calculations
Habitat and biodiversity provision (HabBio)	133	133 million	1
Greenhouse gas sequestration (GHG)	75	75 million	1
Non-consumptive recreation (Recreation)	167	43 million	0.26
Moderation of extreme events (FloodDrought)	124	32 million	0.26
Water purification (Quality)	108	28 million	0.26
Water supply (Supply)	77	20 million	0.26
Recreational hunting and fishing (HuntFish)	6.1	1.6 million	0.26

beaver dams attenuating 3–5 billion (10^9) m^3 of water, assuming one dam per beaver colony (895000–1.5 million dam-building colonies in Table 2) at any one time. During slow water flow, a dam may withhold 30–60% of a stream system's water volume (Kay 1994). Contrastingly, increased baseflow decreases the frequency and duration of drought events (Burchsted et al. 2010, Gibson & Olden 2014). Karran et al. (2017) estimated global beaver ponds to store 2.5–11 billion m^3 of water. Hood and Bayley (2008) showed that beaver presence increases the amount of open water in a landscape ninefold during both wet and dry conditions, but see Westbrook et al. (2006, 2011). The economic gain provided by beaver-created wetlands moderating extreme events amounts to 32 million (dam-builders only) USD(2017) per year (Table 5; variable FloodDrought).

Greenhouse gas sequestration

Wetlands act as greenhouse gas (GHG) sinks and sources, either sequestering or emitting carbon, carbon dioxide and methane, and potentially influencing climate change. Beaver activity causes both sink and source dynamics of carbon and methane, which vary due to the temporal and spatial nature of beaver occupancy, along with dam/flood/pond age and water table level (Lazar et al. 2015, Vehkaoja et al. 2015, Nummi et al. 2018). A single beaver wetland may simultaneously both sequester and emit GHGs if several beaver works are concurrently present (e.g. a dry beaver meadow and a deep inundation area).

Beaver meadows, dams, and ponds endure for extended periods of time and may function as depositories for centuries (Persico & Meyer 2009). Beaver inundations contain large levels of dead wood generated by flooding (Thompson et al. 2016, but see also Misiukiewicz et al. 2018), along with trees felled for dam and lodge construction (Johnston 2017). Beaver activity also influences peat formation, which further modifies GHG dynamics (Nummi et al. 2018), although this aspect remains little studied and unclear. Carbon is also stored in the pond sediments. Carbon storage in beaver meadows may reach 8–23% of estimated total landscape carbon storage (Wohl 2013), and may (Johnston 2014, 2017) or may not (Nummi et al. 2018) be great enough to offset the carbon release of beaver ponds. Nummi et al. (2018) calculated this sequestered carbon in beaver ponds globally to equal 378 Tg.

Calculating the net biogeochemical effects of beaver activity is therefore challenging, making it difficult to assess their role in total GHG budgets. Our meta-regression shows beaver wetlands (dam-builders only) to be worth approximately 75 million USD(2017) per year in GHG sequestration (Table 5; variable GHG).

Water purification

Beaver wetlands act as buffer zones by filtering compounds and human-caused pollutants (heavy metals, disease-causing agents, nitrogen), thus increasing water quality and lessening the costs of downstream wastewater treatment (Skinner et al. 1984, Smith et al. 1991). Filtration in general is a highly beneficial service to societies, and the purifying action of beaver dams (dam-builders only) is worth approximately 28 million USD(2017) per year (Table 5; variable Quality). Savings from natural water filtration services are often compared to the value of investments needed for manual water filtration, as conserving natural wetlands or building artificial ones may decrease the costs incurred to water filtration plants by purifying water prior to it passing through the plant. When quantifying the purification ability of one km^2 of beaver wetland (80000 m^3) in Balodis (1994) with values from Whitfield et al. (2015), beavers (dam-builders only) may aid in purifying ca. 0.8 billion m^3 of water per year.

Provisioning services provided by beavers

Water supply

Water regulation by beaver dams raises groundwater levels both upstream and downstream of the dam. Increases in groundwater storage capacity, water table level, and aquifer recharge have been observed in several studies (e.g. Westbrook et al. 2006, Grygoruk & Nowak 2014). Grygoruk and Nowak (2014) estimated the annual water storage value provided by beavers in Krzemianka Valley, Poland, to approximately equal € 4000. In our meta-regression results, the water supply service totalled 20 million USD(2017) per year (dam-builders only; Table 5; variable Supply).

Recreational hunting and fishing

Extractive goods from beavers include food, materials (castoreum for the perfume industry and pelts), and medicinal resources (castoreum for the natural products industry). Annual harvest levels vary between 1 and 5% in North America, 12% in Europe, and 2% in Russia, which equates to approximately 580000 beavers killed annually in total (Belova et al. 2015, White et al. 2015, Florek et al. 2017, Borisov & Baranov 2018). The large harvest percentage in Europe is influenced by numbers killed in Finland, where North American beavers occur as an invasive species close to, and in certain areas sympatrically with, European beavers (Parker et al. 2012, Alakoski et al. 2019). The lack of accurate hunting data from Russia may well explain the small percentage there; Russian hunting statistics underestimate actual annual hunting levels, meaning that extractive beaver goods are actually more

valuable than our calculations show. Hunting cultures in each of the Northern Hemisphere areas may value different aspects in beaver hunting (meat, pelts, castoreum), and openly accessible information is not available for the percentage of castoreum and beaver meat entering consumer markets in relation to total hunting levels. It is important to remember that products still have value even if they do not enter consumer markets, as hunters can utilise the meat, pelts, and castoreum themselves. Beaver-created wetlands also offer raw material and food output services in the form of improved hunting and fishing opportunities, due to increasing game (e.g. waterfowl, Nummi & Holopainen 2014) and fish (e.g. Schlosser & Kallemeyn 2000) populations occupying these wetlands. Recreational hunting and fishing in beaver wetlands (dam-builders only) is worth 1.6 million USD(2017) per year (Table 5; variable HuntFish).

Supporting services provided by beavers

Habitat and biodiversity provision

Biodiversity as a service is important to human societies because it upholds and regulates ecosystem functioning, stability, resilience, productivity, and nutrient dynamics (Mace et al. 2012, Clark et al. 2014). Decreasing biodiversity diminishes the capability of ecosystems to uphold the services they provide to human society.

Wetlands are important hot spots for species diversity, and as they are globally becoming increasingly rare habitats, the beaver provides habitat and biodiversity provision ecosystem services by aiding in their creation and by increasing habitat heterogeneity (Wright et al. 2002, Hyvönen & Nummi 2008, Nummi & Kuuluvainen 2013, Willby et al. 2018).

An estimated 195000–260000 km^2 of wetlands in the USA have been converted to agriculture and other land-use types during 1835–2000 (Baker & Hill 2003). Whitfield et al. (2015) estimate that, since 2000, beavers have globally created 9500–42000 km^2 of new wetlands, meaning that, since then, global beaver wetlands have compensated for 5–16% of United States wetland loss. A meta-analysis by Stringer and Gaywood (2016) shows the overall positive influence of beavers on biodiversity despite a few negative effects on, e.g., caddisflies (Trichoptera) through decreased lotic conditions, and lamprey (*Lampetra* spp.) and Atlantic salmon (*Salmo salar*) through impeded mobility due to dams.

Beavers may facilitate the rehabilitation and restoration of freshwater habitats in a cost-effective manner (Gorshkov et al. 1999, Kemp et al. 2012). Populations of several aquatic invertebrates, fish, amphibians, waders, ducks, and bats increase in beaver-created habitats (Rosell et al. 2005, Stringer & Gaywood 2016 and references therein), and even entire communities of certain species groups may benefit (Nummi & Holopainen 2014). Beaver wetlands (dam-builders only) contribute ca. 133 million USD(2017) per year to habitat and biodiversity services (Table 5; variable HabBio).

Other nutrient cycling

Gren (1995) suggests that the abatement capacity of a hectare of natural wetlands ranges from 100 to 500 kg nitrogen per year. Several studies have observed beaver ponds to cause reductions in total nitrogen, total phosphorus, and dissolved silicate levels (e.g. by 18, 21, and 32%, respectively; Correll et al. 2000). A beaver dam can withhold 9–6355 m^3 of sediment during its life-span (Nummi et al. 2018), which means that current active dams could hold between 7 million and 9 billion m^3 of sediments during their lifetimes (assuming one pond per colony, 895000–1.5 million dam-building colonies in Table 2). Nutrients are also retained upstream through sediment detainment (Naiman et al. 1994), potentially improving soil quality. This, coupled with increased overbank flooding, provides an important nutrient boost in upstream floodplains (Wohl 2013). Beaver wetlands (dam-builders only) may store 1–7.5 billion kg nitrogen per year when calculated using figures from Gren (1995). We did not find value estimates for the maintenance of soil fertility during our literature search, which is why our meta-analytical function transfer does not include this ecosystem service.

Cultural services provided by beavers

Non-consumptive recreation

Beavers generate habitats suitable for recreation and relaxation, providing, e.g., canoeing and bird-watching possibilities. Generating habitats for recreation may be regarded as a cultural service for recreationists, which not only provides monetary value to societies but also produces mental and physical well-being. In the Northern Hemisphere, recreation in beaver wetlands (dam-builders only) could be worth 43 million USD (2017) per year (Table 5; variable Recreation).

DISCUSSION

We have comprehensively utilised all available knowledge to aggregate information on beaver activity for the Northern Hemisphere, which, to our knowledge, has not been done before. None of the ecosystem services included in our meta-analytical function transfer proved

significant in the calculations, but this only shows that all wetland services in the Northern Hemisphere are valued highly, rather than one or two services being particularly prized. By scaling up the meta-regression coefficients, we show that beavers provide valuable ecosystem services, ranging in value from ca. 1.6 million (recreational hunting and fishing; variable HuntFish) to 133 million (habitat and biodiversity provision; variable HabBio) USD(2017) per year over the whole Northern Hemisphere. The meta-analytical function transfer offers municipality planners and wildlife managers the possibility of roughly estimating local beaver wetland services to aid in beaver management and wetland planning, and scaling up values provides decision-makers with new information that may be incorporated into water management and conservation, such as implementation of the European Union's Water Framework Directive.

In absolute terms, habitat and biodiversity services in beaver wetlands proved to be the most valuable in our analyses, although non-consumptive recreation produced the highest annual per-hectare value. Habitat and biodiversity services benefit society through riparian zone restoration by beavers and increased climate change adaptation caused by increased ecological resilience. Non-consumptive recreation was valued third highest over the whole area. However, our valuation is based on general freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of beaver range in the Northern Hemisphere rather than on specific beaver wetlands, and the distinction may be especially apparent with non-consumptive recreation services. Northern Hemisphere wetlands are considered very important in terms of recreation due to their limited availability (as vast wetland areas have been lost) and high utilisation level. Beaver wetlands, a specific subtype of Northern Hemisphere wetlands, potentially offer less than average recreation services due to their distinct characteristics, i.e. small size, access difficulties and a tendency to become overgrown with vegetation and change in habitat characteristics. Although some recreational sites have been set up specifically to showcase beaver activity and encourage beaver-related nature tourism (e.g. in Scotland, Finland), these generate little income compared with our valuation results. So, despite our efforts to ensure that our meta-regression would not overestimate ecosystem service values, non-consumptive values may indeed be exaggerated.

Several services mitigate the harmful effects of climate change to society, which are projected to worsen in the coming decades. Greenhouse gas sequestration proved to have the second lowest annual per-hectare value, but as the service is not restricted to area or human density it was ascertained to be the second highest in value in absolute terms. How GHG dynamics behave in beaver impoundments is still largely unknown, due to great fluctuations and spatiotemporal variation. The role of GHG sinks and emissions in the ecosystem services concept is concurrently a double-edged sword. While GHG sinks benefit humans in terms of climate change mitigation, it is easy to think that GHG emissions automatically function in an opposite manner. However, GHG dynamics are a natural part of wetland functioning, and therefore, even emissions from beaver wetlands may be seen as ecosystem services. These natural emissions uphold the structure of wetland ecosystems, thereby indirectly creating, e.g., habitat and biodiversity services at local scales. On the other hand, from a global perspective, all GHG emissions, irrespective of whether they are natural or anthropogenic, contribute to climate change, and are therefore disservices. Our meta-analysis only included mineral soil ecosystem service valuations, while beaver activity obviously influences peatland areas as well. Moderation of extreme events and water purification also play a part in alleviating the effects of climate change. Moderation of extreme events proved the third most beneficial in annual per-hectare values, while being fourth most valuable in absolute terms. Increased sediment deposition in beaver wetlands lessens the harmful effects of erosion (Pollock et al. 2017), and periodic overbank flooding upholds hydrological and ecosystem processes in floodplain areas, benefitting, e.g., agriculture (Westbrook et al. 2006), but we were unable to calculate a value for nutrient cycling.

Beaver range is expanding in Europe, and several countries are realising the potential of utilising beaver activity for water management (Törnblom et al. 2011, Kaczyński 2014), wetland restoration (Pollock et al. 2017), and climate change mitigation (Baldwin 2017). Increasing beaver populations bring with them growing benefits and disadvantages; these must be balanced to ensure successful reintroductions and wetland restoration along with social acceptance. Societal utilisation should be maximised, while minimising damage.

Ecosystem services and disservices are scale-dependent. Upholding wetland health and productivity is a public concern, yet the Northern Hemisphere also has significant private ownership of wetlands. Most services provided by beavers and wetlands are free to be enjoyed by society as captured value, often invisibly. On the other hand, costs, i.e. external value, are often accrued to a small group of individuals, who sometimes endure repeated disservices. Beaver activity is also area-dependent, which is why the magnitude of each ecosystem service and disservice provided varies from wetland to wetland and between individuals benefitting or incurring losses. Existing literature and knowledge concerning the ratios

of beaver habitats are deficient, and producing more accurate information on this would help in assessing how various beaver habitats influence the provision of ecosystem services. Beaver management has long been focused on single disservices and how to prevent or mitigate them. When broadening the analysis from individual disservices to landscape-level effects, the number of stakeholders and their interests naturally increases manyfold. Future active beaver management should incorporate a broader horizon, including not only small-scale hindrances, but also a wider paradigm shift towards considering landscape-level and societal effects as well.

The greatest positive outcomes are to be gained when disservices are constrained while concurrently supporting and promoting service provisioning. Tools are needed to ensure landowners gain more than they lose from beaver conservation. Including numerous stakeholder opinions is obviously a complex procedure, but it is possible, if, e.g., Payment for Ecosystem Services schemes are introduced. This could enable stakeholders downstream of a dam or flood zone to compensate landowners at the flood site for benefits gained downstream, while simultaneously offsetting any damages accrued to landowners.

Our study has several limitations. First, our calculations are conditional on how accurate the values are that we have found from the literature. To control the resulting uncertainty, we have used the minimum and maximum values mentioned in the literature and, in the case of beaver population size, we only used the minimum estimate for North American beavers. We also limited our value estimate calculations to dam-building beavers only, i.e. to 50% of the Northern Hemisphere beaver population. These actions help prevent gross overestimations and ensure that our calculations remain conservative. Uncertainty in beaver population sizes also limits our study, as the most recent official estimates for the North American population are several years old. However, this does not affect our per-hectare value estimates, which can be used for estimating the value of individual sites. Meta-analytical value transfer is a method for scaling theoretical values for beaver sites with known areas or populations. Our hemisphere-wide valuations can also be recalculated in the future when more accurate population estimates become available.

Second, as no prior work exists on specifically valuing the ecosystem services of beaver activity, no valuation studies existed for our meta-analytical value transfer. We therefore used studies valuing the ecosystem services provided by freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of the Northern Hemisphere beaver range, which are used to represent beaver habitats. Meta-analytical function transfer is a method specifically designed for valuing services over large areas. The method has previously been used for a similar purpose, e.g. to estimate global wetland value (Woodward & Wui 2001), yet it has limitations in accuracy and consistency. However, to minimise issues with this, we adjusted values from various contexts, e.g. price and income levels, currency data, site area, and study year, into analogous units. Also, to avoid any potential issues with double counting, we did not aggregate all ecosystem service values into one total value.

Third, we were only able to utilise English-language sources in our value transfer, meaning that we may have missed some texts valuing local wetland ecosystem services. Fourth, we were unable to quantify the value of beaver activity in terms of nutrient cycling or historical value, as none of the documents in our meta-analytical function transfer included estimates on these particular ecosystem services. Fifth, our results may show aggregation bias, which prevents the statistical analyses from uncovering significant differences between the explanatory variables. However, we do not consider this to be a large problem, as the wider idea of our study is to help managers and decision-makers recognise and even determine the approximate values of individual beaver sites. Sites are highly variable, so they are not identical in which services they provide and to what degree. Our per-hectare values are therefore useful for estimating how much an area may be worth in terms of predetermined ecosystem services, and for comparing benefits with potential disservices.

CONCLUSIONS

Understanding how the economic impacts of beaver activity function and are defined is imperative for improving the future management of beaver populations. Until now, no attempts have been made to quantify the positive effects of beaver activity in one study. Our aim was to expand on and consolidate previous research to gain a large-scale perception of the value of beaver activity, and also to produce value estimates that future researchers may use for estimating the economic value of individual beaver sites or sites in larger geographic areas. The importance of and need for all-encompassing management and planning may very well expand in the future, as beaver populations continue growing in Eurasia, and individuals and colonies spread into increasingly urban areas and human habitation persistently encroaches on beaver habitat.

This study is a first attempt at gaining an idea of ecosystem services provided by beavers. We show that habitat and biodiversity, non-consumptive recreation, and moderation of extreme events are particularly valuable services. Though the North American beaver population is currently stable, the Eurasian beaver population is increasing, which

will lead to increasing benefits and disadvantages from beaver activity. These must be balanced to ensure social acceptance of the species and to maximise social welfare while damage is minimised. In a future of increasing climatic uncertainty, beavers may play a notable role in stabilising hydrological conditions. Implementing Payment for Ecosystem Services schemes to utilise the positive aspects of beaver activity is possible and offers a concrete way for societies to benefit while mitigating the economic losses accrued to landowners. However, questions remain, particularly concerning the biogeochemical effects of beaver wetlands. Currently, the scientific research community has no clear picture of how beavers affect GHG dynamics. More studies should be conducted on how the trade-offs between GHG emissions and sequestration function. Markets exist for these ecosystem services (Ezzine-de-Blas et al. 2016), and understanding how these services behave in beaver wetlands is an important next step.

ACKNOWLEDGEMENTS

This study was funded by the Kone Foundation, the Maj and Tor Nessling Foundation, and the Emil Aaltonen Foundation. We sincerely thank Niko Kulha (Finnish Environment Institute) and Matti Mäntynen (Metsähallitus) for assistance with the geographic information system analyses.

REFERENCES

Alakoski R, Kauhala K, Selonen V (2019) Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. *Biological Invasions* 21: 1601–1613.

Baker BW, Hill EP (2003) Beaver (*Castor canadensis*). In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild Mammals of North America: Biology, Management, and Conservation*, 288–310. 2nd ed. The John Hopkins University Press, Baltimore, Maryland, USA.

Baldwin J (2017) Institutional obstacles to beaver recolonization and potential climate change adaptation in Oregon, USA. *Yearbook of the Association of Pacific Coast Geographers, University of Hawai'i Press* 79: 93–114.

Balodis M (1994) Beaver population of Latvia: history, development and management. *Proceeding of the Latvian Academy of Sciences B 7/8* 122–127.

Belova O, Sjöberg G, Ecke F, Lode E, Thorell D (2015) *Beaver Population Management in the Baltic Sea Region - a Review of Current Knowledge, Methods and Areas for Development*, 1–50. European Regional Development Fund Interreg Baltic Sea Region. https://www.skogsstyrelsen.se/globalassets/projektwebbplatser/wambaf/beaver/reviews/beaver-tool-short-document.pdf.

Bhat M, Huffaker RG, Lenhart SZ (1993) Controlling forest damage by dispersive beaver populations: centralized optimal management strategy. *Ecological Applications* 3: 518–530.

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) *Introduction to Meta-Analysis*. John Wiley & Sons, Oxford, UK.

Borisov BP, Baranov VN (2018) European beaver. In: *Status of Hunting Resources in the Russian Federation in 2008–2013*. FGBU Centrokhotcontrol (in Russian). http://www.ohotcontrol.ru/resource/Resources_2008-2013/Resources_2008-2013.php.

Boyd J, Banzhaf S (2007) What are ecosystem services? The need for standardized environmental accounting units. *Ecological Economics* 63: 616–626.

Brander L (2006) *Guidance Manual on Value Transfer Methods for Ecosystem Services*. United Nations Environment Programme UNEP, Publishing Services Section, UNON, Nairobi, Kenya.

Buckley M, Souhlas T, Niemi E, Warren E, Reich S (2011) *The Economic Value of Beaver Ecosystem Services. Escalante River Basin, Utah*. ECONorthwest, Portland, Oregon, USA.

Burchsted D, Daniels M, Thorson R, Vokoun J (2010) The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience* 60: 908–922.

Center for International Earth Science Information Network - CIESIN - Columbia University (2017) *Gridded Population of the World, Version 4 (GPWv4): Population Count, Revision 10*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, New York, USA. 2019, https://doi.org/10.7927/H4PG1PPM. Accessed 20 February.

Chaikumbung M, Scarborough H (2016) The economic value of wetlands in developing countries: a meta-regression analysis. *Ecological Economics* 124: 164–174.

Clark NE, Lovell R, Wheeler BR, Higgins SL, Depledge MH, Norris K (2014) Biodiversity, cultural pathways, and human health: a framework. *Trends in Ecology & Evolution* 29: 198–204.

Correll DL, Jordan TE, Weller DE (2000) Beaver pond biogeochemical effects in the Maryland Coastal Plains. *Biogeochemistry* 49: 217–239.

Danilov PI, Fyodorov FV (2015) Comparative characterization of the building activity of Canadian and European beavers in Northern European Russia. *Russian Journal of Ecology* 46: 272–278.

Deeks JJ, Higgins JPT, Altman DG (2019) Analysing data and undertaking meta-analyses. In: Higgins JPT, Thomas J, Chandler J, Cumpston M, Li T, Page MJ, Welch VA (eds) *Cochrane Handbook for Systematic Reviews of Interventions Version 6.0 (updated July 2019)*. Cochrane.

www.training.cochrane.org/handbook. Accessed 15 February 2020.
ESA Globcover (2009) *Global Landcover Map*. http://due.esrin.esa.int/page_globcover.php.
Ezzine-de-Blas D, Wunder S, Ruiz-Pérez M, Moreno-Sanchez RdP (2016) Global patterns in the implementation of payments for environmental services. *PLoS One* 11(3): e0149847.
Farley J, Costanza R (2010) Payments for ecosystem services: from local to global. *Ecological Economics* 69: 2060–2068.
Florek M, Drozd L, Skałecki P, Domaradzki P, Litwińczuk A, Tajchman K (2017) Proximate composition and physicochemical properties of European beaver (*Castor fiber* L.) meat. *Meat Science* 123: 8–12.
Gibson P, Olden J (2014) Ecology, management, and conservation implications of North American beaver *(Castor canadensis)* in dryland streams. *Aquatic Conservation Marine and Freshwater Ecosystems* 24: 391–409.
Gorshkov YA, Easter-Pilcher AL, Pilcher BK, Gorshkov D (1999) Ecological restoration by harnessing the work of beavers. In: Busher PE, Dzieciolowsk RM (eds) *Beaver Protection, Management, and Utilization in Europe and North America*, 67–76. Kluwer Academic/Plenum Publishers, New York, USA.
Gren I-M (1995) The value of investing in wetlands for nitrogen abatement. *European Review of Agricultural Economics* 22: 157–172.
Grunewald K, Bastian O (eds; 2015) *Ecosystem Services: Concept, Methods and Case Studies*. Springer-Verlag, Berlin, Heidelberg, Germany.
Grygoruk M, Nowak M (2014) Spatial and temporal variability of channel retention in a lowland temperate forest stream settled by European beaver (*Castor fiber*). *Forests* 5: 2276–2288.
Guillozet K (2015) Shade trading: an emerging riparian forest-based payment for ecosystem services market in Oregon, USA. *Environmental Management* 56: 957–970.
Gustavson K, Kennedy E (2010) Approaching wetland valuation in Canada. *Wetlands* 30: 1065–1076.
Haines-Young R, Potschin MB (2018) *Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure*. http://www.cices.eu.
Halley DJ, Rosell F, Saveljev A (2012) Population and distribution of Eurasian beaver (*Castor fiber*). *Baltic Forestry* 18: 168–175.
Halley DJ, Saveljev AP, Rosell F (2021) Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. *Mammal Review* 51(1).
Hood GA, Bayley SE (2008) Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation* 141: 556–567.
Hyvönen T, Nummi P (2008) Habitat dynamics of beaver *Castor canadensis* at two spatial scales. *Wildlife Biology* 14: 302–308.
Johnston CA (2014) Beaver pond effects on carbon storage in soils. *Geoderma* 213: 371–378.
Johnston CA (2017) *Beavers: Boreal Ecosystem Engineers*. Springer International Publishing, Basel, Switzerland.
Kaczyński P (2014) *Beaver-made Damming Constructions - Cost-effective Way to Accumulate Water in Small-scale Retention Program in Poland?* Report No. 8, Baltic Landscape. Baltic Sea Region. report-no-08-wp-5-and-6-p-kaczynski-march-2014-beaver-made-damming-constructions.pdf.
Karran DJ, Westbrook CJ, Wheaton JM, Johnston CA, Bedard-Haughn A (2017) Rapid surface-water volume estimations in beaver ponds. *Hydrology and Earth System Sciences* 21: 1039–1050.
Kay CE (1994) Impact of native ungulates and beaver on riparian communities in the intermountain west. *Natural Resources and Environmental Issues* 1: 1–22.
Kemp PS, Worthington TA, Langford TEL, Tree ARJ, Gaywood MJ (2012) Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries* 13: 158–181.
Lazar J, Addy K, Gold A, Groffman P, McKinney R, Kellogg D (2015) Beaver ponds: resurgent nitrogen sinks for rural watersheds in the Northeastern United States. *Journal of Environmental Quality* 44: 1684–1693.
Liu S, Constanza R, Farber S, Troy A (2010) Valuing ecosystem services - theory, practice, and the need for a transdisciplinary synthesis. *Annals of the New York Academy of Sciences* 1185: 54–78.
Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multi-layered relationship. *Trends in Ecology & Evolution* 27: 19–26.
Millennium Ecosystem Assessment (2005a) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC, USA.
Millennium Ecosystem Assessment (2005b) *Ecosystems and Human Well-being: Wetlands and Water: Synthesis*. World Resources Institute, Washington, DC, USA.
Misiukiewicz W, Piętka S, Bielinis E (2018) Impact of the European beaver *Castor fiber* on deadwood resources in lowland river valley – a case study in Wigry National Park (NE Poland). *Polish Journal of Ecology* 66: 270–285. https://doi.org/10.3161/15052249PJE2018.66.3.007.
Naiman RJ, Pinay G, Johnston CA, Pastor J (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75: 905–921.
Nummi P, Holopainen S (2014) Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. *Aquatic Conservation* 24: 623–633.

Nummi P, Kuuluvainen T (2013) Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. *Boreal Environment Research* 18(Suppl: A):13–24.

Nummi P, Vehkaoja M, Pumpanen J, Ojala A (2018) Beavers affect carbon biogeochemistry: both short-term and long-term processes are involved. *Mammal Review* 48: 298–311.

Parker H, Nummi P, Hartman G, Rosell F (2012) Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. *Wildlife Biology* 18: 354–365.

Persico L, Meyer G (2009) Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park, Wyoming. *Quaternary Research* 71: 340–353.

Pollock MM, Lewallen G, Woodruff K, Jordan CE, Castro JM (eds; 2017) *The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains. Version 2.0*. United States Fish and Wildlife Service, Portland, Oregon, USA. https://www.fws.gov/oregonfwo/promo.cfm?id=177175812.

Ramsar Convention on Wetlands (2018) *Global Wetland Outlook: State of the World's Wetlands and their Services to People*. Ramsar Convention Secretariat, Gland, Switzerland.

Reynaud A, Lanzanova D (2017) A global meta-analysis of the value of ecosystem services provided by lakes. *Ecological Economics* 137: 184–194.

Rosell F, Bozsér O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35: 248–276.

Russi D, ten Brink P, Farmer A, Badura T, Coates D, Förster J, Kumar R, Davidson N (2013) *The Economics of Ecosystems and Biodiversity for Water and Wetlands*. IEEP and Ramsar Secretariat, London, UK and Brussels, Belgium, Gland, Switzerland.

Schlosser IJ, Kallemeyn LW (2000) Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecological Society of America* 81: 1371–1382. https://doi.org/10.1890/0012-9658(2000)081[1371:SVIFAA]2.0.CO;2.

Schuyt K, Brander L (2004) *Living Waters: Conserving the Source of Life: the Economic Values of the World's Wetlands*. WWF Report, Gland, Switzerland.

Siemer WF, Jonker SA, Decker DJ, Organ JF (2013) Toward an understanding of beaver management as human and beaver densities increase. *Human-Wildlife Interactions* 7: 114–131.

Skinner QD, Speck JE Jr, Stream M, Adams JC (1984) Water quality as influenced by beaver within grazing systems in Wyoming. *Journal of Range Management* 37: 142–146.

Smith ME, Driscoll CT, Wyskowski BJ, Brooks CM, Cosentini CC (1991) Modification of stream ecosystem structure and function by beaver *(Castor canadensis)* in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69: 56–61.

Stringer A, Gaywood M (2016) The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review* 46: 270–283.

Thompson S, Vehkaoja M, Nummi P (2016) Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management* 360: 1–8.

Törnblom J, Angelstam P, Hartman G, Henrikson L, Sjöberg G (2011) Toward a research agenda for implementation: knowledge about beaver (*Castor fiber*) as a tool for water management with a catchment perspective. *Baltic Forestry* 17: 154–161.

Touihri M, Labbé J, Imbeau L, Darveau M (2018) North American Beaver (*Castor canadensis* Kuhl) key habitat characteristics: review of the relative effects of geomorphology, food availability and anthropogenic infrastructure. *Ecoscience* 25: 9–23.

Vehkaoja M, Nummi P, Rask M, Tulonen T, Arvola L (2015) Spatiotemporal dynamics of boreal landscapes with ecosystem engineers: beavers influence the biogeochemistry of small lakes. *Biogeochemistry* 124: 405–415.

Westbrook CJ, Cooper DJ, Baker BW (2006) Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. *Water Resource Research* 42: 1–12.

Westbrook CJ, Cooper DJ, Baker BW (2011) Beaver assisted river valley formation. *River Research and Applications* 27: 247–256.

White HB, Decker T, O'Brien MJ, Organ JF, Roberts NM (2015) Trapping and furbearer management in North American wildlife conservation. *International Journal of Environmental Studies* 72: 756–769.

Whitfield CJ, Baulch HM, Chun KP, Westbrook CJ (2015) Beaver-mediated methane emission: the effects of population growth in Eurasia and the Americas. *Ambio* 44: 7–15.

Willby NJ, Law A, Levanoni O, Foster G, Ecke F (2018) Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B* 373: 20170444.

Wohl E (2013) Landscape-scale carbon storage associated with beaver dams. *Geophysical Research Letters* 40: 3631–3636.

Woodward R, Wui Y-S (2001) The economic value of wetland services: a meta-analysis. *Ecological Economics* 37: 257–270.

World Bank (2018) *World Development Indicators*. The World Bank Group. http://data.worldbank.org/data-catalog/world-development-indicators. Accessed December 2018.

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132: 96–101.

Zav'yalov N (2011) Settlement history, population dynamics and the ecology of beavers (*Castor fiber* L) in the Darwin reserve. In: Sjöberg G, Ball J (eds) *Restoring the European Beaver: 50 Years of Experience*. Pensoft Publishers, Sofia, Bulgaria.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Ecosystem service valuation sources used for the literature review.

Appendix S2. Primary valuation studies used in the meta-analytical function transfer.

Biol Invasions (2020) 22:663–680
https://doi.org/10.1007/s10530-019-02120-8

ORIGINAL PAPER

Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass (*Bromus tectorum*) in the central Great Basin, USA

Matthew A. Williamson · Erica Fleishman · Ralph C. Mac Nally · Jeanne C. Chambers · Bethany A. Bradley · David S. Dobkin · David I. Board · Frank A. Fogarty · Ned Horning · Matthias Leu · Martha Wohlfeil Zillig

Received: 27 December 2018 / Accepted: 1 November 2019 / Published online: 8 November 2019
© Springer Nature Switzerland AG 2019

Abstract Cheatgrass (*Bromus tectorum*) has increased the extent and frequency of fire and negatively affected native plant and animal species across the Intermountain West (USA). However, the strengths of association between cheatgrass occurrence or abundance and fire, livestock grazing, and precipitation are not well understood. We used 14 years of data from 417 sites across 10,000 km^2 in the central Great Basin to assess the effects of the foregoing predictors on cheatgrass occurrence and prevalence (i.e., given occurrence, the proportion of measurements in which the species was detected). We implemented hierarchical Bayesian models and considered covariates for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 as strongly associated with the response variable. Similar to previous research, our models indicated that fire is a strong, positive predictor of cheatgrass occurrence and prevalence. Models fitted to all sample points and to only unburned points indicated that grazing and the proportion of years grazed were strong positive predictors of occurrence and prevalence. In contrast, in models restricted to burned points, prevalence was high, but decreased slightly as the proportion of years grazed increased (relative to other burned points). Prevalence of cheatgrass also decreased as the prevalence of perennial grasses increased. Cheatgrass occurrence decreased as elevation increased, but

M. A. Williamson (✉)
Boise State University, Boise, ID 83725, USA
e-mail: mattwilliamson@boisestate.edu

M. A. Williamson · E. Fleishman · F. A. Fogarty · M. Wohlfeil Zillig
University of California, Davis, CA 95616, USA

E. Fleishman
Colorado State University, Fort Collins, CO 80523, USA

R. C. Mac Nally
Institute for Applied Ecology, University of Canberra, Bruce, ACT 2617, Australia

R. C. Mac Nally
School of BioSciences, The University of Melbourne, Parkville, VIC 3052, Australia

J. C. Chambers · D. I. Board
Rocky Mountain Research Station, USDA Forest Service, Reno, NV 89512, USA

B. A. Bradley
University of Massachusetts, Amherst, MA 01003, USA

D. S. Dobkin
High Desert Ecological Research Institute, Bend, OR 97702, USA

N. Horning
American Museum of Natural History, New York, NY 10024, USA

M. Leu
College of William and Mary, Williamsburg, VA 23185, USA

prevalence within the elevational range of cheatgrass increased as median winter precipitation, elevation, and solar exposure increased. Our novel time-series data and results indicate that grazing corresponds with increased cheatgrass occurrence and prevalence regardless of variation in climate, topography, or community composition, and provide no support for the notion that contemporary grazing regimes or grazing in conjunction with fire can suppress cheatgrass.

Keywords *Bromus tectorum* · Hierarchical models · Fire · Great Basin · Livestock grazing · Resilience

Introduction

Increases in the distribution and abundance of non-native grasses have modified fire dynamics worldwide, often leading to loss of human life and property and to substantial financial costs (D'Antonio and Vitousek 1992; Brooks et al. 2004). Cheatgrass (*Bromus tectorum*), an annual grass native to Eurasia, has increased in abundance and geographic distribution across the Intermountain West (USA) in recent decades. For example, the cover of cheatgrass is estimated to be at least 15% across about 210,000 km^2 of the Great Basin, a $>$ 425,000 km^2 desert within the Intermountain West (Bradley et al. 2018). As cheatgrass expands, it drives a cycle of increases in the frequency and extent of fire and further expansion of cheatgrass (Bradley et al. 2018). The area burned has increased by as much as 200% since 1980, accompanied by over US$1 billion in fire-suppression costs (Balch et al. 2013; NCEI 2018). Cheatgrass-induced changes in fire patterns are associated with loss of sagebrush (*Artemisia* spp.), perennial grasses, and forbs that provide habitat for hundreds of plant and animal species. These species include Greater Sage-Grouse (*Centrocercus urophasianus*), which repeatedly has been considered for listing under the U.S. Endangered Species Act (Freeman et al. 2014; USFWS 2015; Germino et al. 2016).

Although the effects of cheatgrass on fire dynamics are well known, the effects of some potential predictors of cheatgrass distribution and abundance at large spatial extents, such as livestock grazing, abundance of native perennial grasses, precipitation, elevation, and solar exposure, are less clear. For example, it has been suggested that livestock grazing, a major land use in the region, directly and indirectly (e.g., through reductions in the abundance of native perennials) increases the likelihood of invasion (e.g., Reisner et al. 2013). Moreover, the strength of response of both cheatgrass occurrence and prevalence (the proportion of binary occurrence measurements in a given area in which a species is present, and a critical component of the species' effects; Parker et al. 1999) to fire, grazing, and precipitation are unknown. We aimed to clarify these relations.

Several studies assessed environmental correlates of cheatgrass cover, density, or abundance in the Intermountain West (e.g., Gelbard and Belnap 2003; Bradley and Mustard 2006; Compagnoni and Adler 2014; Pilliod et al. 2017). These correlates vary across the range of cheatgrass (e.g., Bradley et al. 2016; Brooks et al. 2016), in relation to fire, and potentially over time. The cover, density, or abundance of cheatgrass can increase rapidly in areas that recently have burned or been disturbed by land uses such as road construction, maintenance, or use; agricultural activities; or grazing by domestic livestock (Mack 1981; Bradley and Mustard 2006; Banks and Baker 2011; Reisner et al. 2013; Pyke et al. 2016; Svejcar et al. 2017).

Previous field research rarely quantified the links between cheatgrass and livestock grazing due to the difficulty of obtaining reliable, quantitative data regarding this land use. Yet management of livestock grazing on the public lands that cover more than half of the Intermountain West, and about 75% of the Great Basin, may have a substantial effect on the expansion and ecological effects of cheatgrass. Livestock trample soil crusts, which can increase potential colonization by cheatgrass; feed on native perennial grasses that can compete with cheatgrass (see below); and disperse cheatgrass seeds (Reisner et al. 2013). In many cases, the US Forest Service (USFS) and US Bureau of Land Management (BLM)—the agencies with jurisdiction over the majority of public lands in the western United States—defer continuation of livestock grazing on active allotments for 2 years following fire (BLM 2007). Although there are advocates for both shorter and longer exclusion periods, there are few empirical data to inform management decisions, especially in areas where cheatgrass has become widespread.

The abundance and cover of native perennial grasses that compete with cheatgrass independent of land use also are directly and negatively associated with the intensity of livestock grazing (Adler et al. 2005; Reisner et al. 2013). These grasses did not coevolve with high abundances of large ungulates (Mack and Thompson 1982). Although fires in Great Basin ecosystems typically remove fire-intolerant shrubs such as sagebrush, most native perennial grasses survive. The cover of cheatgrass and other non-native annual, invasive grasses is negatively related to the cover of perennial native grasses following prescribed fire and other management actions (Davies 2008; Chambers et al. 2014; Roundy et al. 2018). For example, in areas dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), about 20% cover of perennial, native forbs and grasses is necessary to prevent increases in the cover of annual, invasive grasses after prescribed fire treatments (Chambers et al. 2014; Roundy et al. 2018). Therefore, livestock-grazing history and the abundance of perennial native grasses are likely to be associated with cheatgrass presence and abundance, and to interact with fire.

Establishment of cheatgrass is associated with relatively high levels of precipitation during autumn or spring, which facilitate the species' germination and growth (Bradley et al. 2016). Percent cover and biomass of cheatgrass also are highly responsive to heavy winter and spring precipitation (Knapp 1998). Cheatgrass biomass can increase tenfold following wet winters (Garton et al. 2011), substantially increasing fine-fuel loads and the probability of fire (Balch et al. 2013; Pilliod et al. 2017). Biomass of cheatgrass may remain high during the year following a wet winter, especially when competition from perennial grasses is low (Bradley et al. 2016). There is some evidence that the abundance of cheatgrass is less likely to increase in areas with relatively high summer precipitation and cool annual temperatures (Taylor et al. 2014; Brummer et al. 2016). Therefore, precipitation is likely to be associated with the presence and abundance of cheatgrass.

Cheatgrass occurs over extensive topographic gradients (Brooks et al. 2016), but the likelihood of presence or the abundance of cheatgrass generally decreases as elevation increases (Compagnoni and Adler 2014; Chambers et al. 2016). For example, in both 1973 and 2001, probability of cheatgrass presence in the central Great Basin was highest at elevations from 1200 to 1400 m (Bradley and Mustard 2006). Between those years, cheatgrass expanded into lower elevations, but did not expand at elevations above 1700 m, and the probability of cheatgrass presence above 2500 m was almost zero (Bradley and Mustard 2006). The mechanisms underlying the relation between cheatgrass presence or abundance and elevation are fairly well understood. Germination, growth, and reproduction of cheatgrass generally are highest at intermediate elevations with moderate temperatures and water availability, limited at low elevations by relatively high temperatures and low precipitation, and limited at high elevations by low soil temperatures (Meyer et al. 2001; Chambers et al. 2007, 2017; Compagnoni and Adler 2014). Strong competitive interactions between perennial grasses and cheatgrass affect density and cover of cheatgrass across elevational gradients (Chambers et al. 2007; Reisner et al. 2013; Larson et al. 2017). Soil moisture and nutrient levels generally increase as elevation increases, leading to an increase in primary productivity and higher levels of competition between cheatgrass and other species (Chambers et al. 2007; Compagnoni and Adler 2014).

Some work has suggested that cheatgrass is more likely to be present and abundant on certain topographic aspects, although relations with aspect may vary across the Great Basin and among assessment methods. On the basis of Landsat data for the central Great Basin, Bradley and Mustard (2006) found that likelihood of cheatgrass presence was greatest on west- and northwest-facing slopes. However, fine-resolution empirical analyses in the northern Great Basin and in the Rocky Mountains suggested that cheatgrass abundance was greatest on south-facing slopes (Banks and Baker 2011; Svejcar et al. 2017), especially at relatively high elevations (Brooks et al. 2016).

Here, we use a 14-year time-series of data collected within a bounding area of $\sim$ 10,000 km^2 of the central Great Basin (Fig. 1) to assess empirically the relative strengths of association of cheatgrass occurrence and prevalence with fire, livestock grazing, precipitation, and other abiotic environmental conditions. Our selection of predictor variables was motivated by the ecological theories and previous research summarized above, and facilitated by the unusually extensive topographic gradients and duration covered

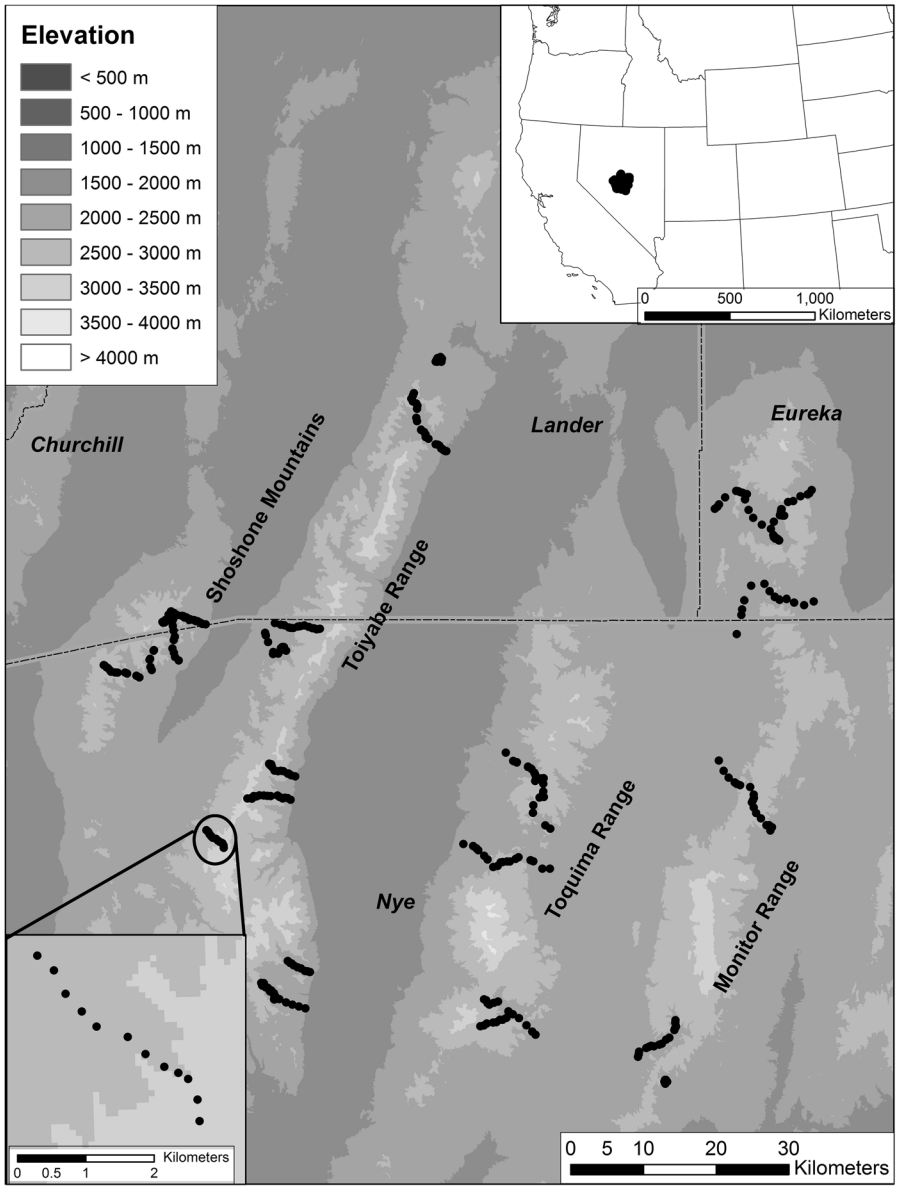


Fig. 1 Locations of the 417 sample points that were distributed among 29 canyons in four mountain ranges in the central Great Basin (Lander, Eureka, and Nye Counties, Nevada, USA). We sampled cheatgrass at each point for a minimum of three years and a maximum of eight years

by our data. Our ultimate aim is to inform policy and management actions that may minimize the further expansion and undesirable direct and indirect effects of cheatgrass on species and ecosystem function across the Intermountain West. Our results also may inform research priorities or sampling designs to more thoroughly examine interactive effects of drivers of cheatgrass colonization and dominance.

Methods

Data collection and development

We used two sets of data collected from 2001 through 2015 in 29 canyons in four mountain ranges (Shoshone, Toiyabe, Toquima, and Monitor) in Lander, Nye, and Eureka Counties, Nevada (Fleishman 2015) (Fig. 1). Within those canyons, we sampled cheatgrass at elevations from 1886 through 3219 m over a range of disturbance histories. Complete

vegetation data and metadata are in Chambers et al. (2010) and Fleishman (2015). Detailed information about data collection methods also is in Urza et al. (2017).

First, we collected data on cheatgrass and other elements of vegetation structure and composition from 30 to 50 m point-intercept transects (10–31 locations per transect per year) along elevational gradients of the 29 canyons. We refer to each transect as a *sample point*. We collected data from each sample point for 3–8 years from 2001 to 2015.

Second, we collected vegetation data in three pairs of adjacent alluvial fans on burned and unburned sites at elevations of 2073, 2225, and 2347 m on a north-facing slope within one watershed in the Shoshone Mountains. We established three sampling plots of ca 0.1 ha within burned and unburned plots at each elevation. We measured areal cover of herbaceous species and shrubs within 50, 2-m^2 quadrats per plot in 2001, prior to a prescribed fire. We remeasured the same plots in 2002, 2004, and 2006, after the fire. We measured areal cover of herbaceous species within 25–30, 0.25-m^2 quadrats. We converted these quadrats to presence–absence estimates for a sample point assigned to the geographic center of the plots to allow combination with the transect data (i.e., the number of the 50 quadrats in which cheatgrass was detected).

We assessed cheatgrass occurrence by considering sample points at which cheatgrass was not recorded during the study period as absences, and sample points at which cheatgrass was recorded present in $\geq$ 1 year during the study period as presences. For each sample point at which cheatgrass was recorded present, we estimated local prevalence of cheatgrass by summing the number of point intercepts (or quadrats) where cheatgrass was recorded present and comparing that to the total number of point intercepts (or quadrats) taken at each point in a given year.

We characterized the grazing and fire history of each sample point for each year during the period in which we collected vegetation data. Each year from 2001 through 2015, EF or JC made multiple visits (generally 3–6) to each point at which data were collected and recorded whether it was grazed by domestic cattle and whether a fire occurred during the growing season or between the previous and current growing season. We augmented these observations with information on whether grazing by domestic cattle was permitted on each allotment (i.e., whether the allotment was active) from 2006 through 2015 (M. West, USFS, personal communication). We assigned a binary value to indicate whether the allotment in which a given sample point was embedded was grazed during each year. Because data on realized (as opposed to permitted) grazing intensity are not maintained by the USFS, which manages virtually all of the land on which our sample points were located, we assumed that all active allotments were grazed. Although permitees may use a portion of an allotment rather than an entire allotment, or engage in short-term non-use of an allotment, it is reasonable to assume that active allotments were grazed recently or during the years in which data were collected. We calculated the proportion of years during which each sample point was grazed (years grazed/years during the study period prior to collection of data in a given year) to estimate levels of livestock use. We classified sampled points as burned if a fire occurred at the sample point from 2000 through 2015.

For burned points, we calculated the number of growing seasons between the fire and a given field sample. We included both linear and quadratic terms for number of growing seasons between the fire and the sampling event because Miller et al. (2013) suggested that cheatgrass could decrease in abundance after about 12 years if the abundance of other grasses, forbs, and shrubs increases. To examine the potential effect on cheatgrass of competition from perennial native grasses, we also estimated the prevalence of perennial native grasses at each sample point by summing the number of points along transects or within quadrats at which perennial native grass was recorded present and dividing by the total number of points.

We derived the elevation of each sample point from the 10-m National Elevation Dataset (lta.cr.usgs.gov/NED). We calculated a hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded) in ArcGIS 10.4 (Esri, www.esri.com/en-us/home) for each sample point (at the geographic center of transects or quadrats) on the basis of the sun angle and azimuth at the center of study area on 21 June at 15:00. The date and time represent maximum solar exposure on summer solstice (Blackard and Dean 1999). Values of the hillshade index ranged from 0 to 254, with higher values indicating greater solar exposure on southwest-facing slopes. We estimated solar radiation on the basis of a hillshade index

Table 1 Predictors included in models of the probability of presence (occurrence) of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Model	Level	Predictor
Occurrence		
All sample points	Point	Elevation
		Hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded)
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no) (whether a fire occurred during the growing season or between the previous and current growing season)
		Grazed (yes/no) (whether grazing by domestic cattle was permitted on the allotment within which the point was located)
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Grazed (yes/no)
Prevalence		
All points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no)
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Burned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual spring precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Time since fire
		Time since fire^2
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling

rather than aspect because it is difficult to differentiate between opposite aspects (e.g., north vs. south or east vs. west) within a statistical model. We estimated precipitation at each sample point with data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM). We calculated both cumulative precipitation in the winter (1 October–31 March) and spring (1 April–30 June) preceding sampling and the proportion of precipitation in those two seasons that fell in winter. We included the latter variable to distinguish associations with precipitation seasonality from those with cumulative precipitation.

We restricted the data to years for which data on cheatgrass and predictors were available for each sample point. In some cases, the bivariate correlation between winter and spring precipitation was > 0.7. We retained the precipitation estimate that had the lowest correlation with all other predictors in the model. We scaled all predictors to a mean of zero and unit variance to facilitate model convergence and to represent the predictors on a common scale.

Statistical modeling

We modeled associations between predictors and occurrence across the 14-year study period, and between predictors and annual variation in prevalence throughout the 14-year study period. To evaluate associations with predictors in the presence and in the absence of fire, we applied these models to (1) all of the data ($N_{occurrence} = 417, N_{prevalence} = 624$), (2) only those points that had not been burned ($N_{occurrence} = 326, N_{prevalence} = 314$), and (3) only those points that had been burned ($N_{occurrence} = 91, N_{prevalence} = 310$). We did not fit occurrence models to burned points because cheatgrass was recorded present in 88 of those 91 points, preventing the model from discriminating between the determinants of presence and absence.

We classified sample points as *recorded present* if cheatgrass was detected at any time during the study period (occurrence = 1) and *recorded absent* if cheatgrass was not observed during the study period (occurrence = 0). We used a Bernoulli response model to link occurrence with candidate predictors (Table 1). We then used a binomial response model to identify predictors that were associated strongly with the prevalence of cheatgrass in the sample points at which cheatgrass was recorded. We used separate response models rather than zero-inflated models (e.g., hurdle models sensu Mullahy 1986) because the spatial–temporal processes almost certainly are not statistically stationary. Hurdle models assume that occurrence is stationary, but cheatgrass is still spreading throughout our study area.

Cheatgrass occurrence

For each sample point, we calculated winter and spring precipitation as the median annual value across the study period. We assigned binary values for fire and grazing that reflected whether the point had been burned or grazed in any year of the study period prior to the year in which cheatgrass first was recorded present or, if cheatgrass consistently was recorded absent, the final year of sampling.

We modeled whether cheatgrass was recorded present ($\Phi_{i,j,k,s}$) during a given year (i) at sample point j within canyon k within mountain range s as the outcome of a Bernoulli trial with probability $p_{i,j,k,s}$. We modeled probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{j,k,s}$) and the product of observation-level regression parameters (β_{obs}) and observation-level standardized predictors (some predictors vary among years; $\boldsymbol{X}_{obs}$, Table 1).

$$\Phi_{i,j,k,s} \sim Bernoulli\left(p_{i,j,k,s}\right), \tag{1}$$

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{2}$$

We modeled the point-level intercepts as the outcome of a canyon- and range-specific, point-level intercept ($\alpha_{k,s}$) and the sample point-level regression parameters (β_{point}) and sample point-level predictors (i.e., predictors with values that were constant throughout the study period, $\boldsymbol{X}_{point}$, Table 1).

$$\alpha_{j,k,s} \sim Normal\left(\mu_{j,k,s}, \sigma_{k,s}\right), \tag{3}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}\boldsymbol{X}_{point}, \tag{4}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{5}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal\left(\mu_{k,s}, \sigma_{s}\right), \tag{6}$$

$$\mu_{k,s} = \alpha_s, \tag{7}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{8}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{9}$$

$$\mu_0 \sim Normal(0, 2), \tag{10}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{11}$$

This hierarchical structure accounted for potential systematic variation among points within the same canyon and among canyons within the same mountain range, and for potential spatial organization in the data.

Cheatgrass prevalence

For sample points at which cheatgrass was recorded present, we modeled cheatgrass prevalence as functions of topographic, climatic, and land-use variables (Table 1). We attributed observation-level predictor values to each point for the corresponding year of sampling. We included the annual estimate of each precipitation variable as an observation-level predictor and the median of the annual values of each precipitation variable throughout the study period as a point-level predictor. We used the proportion of years grazed as the grazing predictor in these analyses.

We modeled the prevalence of cheatgrass ($y_{i,j,k,s}$) in a given year (i) at sample point j within canyon k within mountain range s as the binomial outcome of the number of detections, which in turn was a function of the number of samples taken at that point in that year ($n_{i,j,k,s}$), where cheatgrass is present with probability $p_{i,j,k,s}$. We modeled the probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{i,j,k,s}$) and the product of an array of observation-level slope parameters (β_{obs}) and observation-level predictors ($\boldsymbol{X}_{obs}$, Table 1).

$$y_{i,j,k,s} \sim Binomial\left(n_{i,j,k,s}, p_{i,j,k,s}\right), \tag{12}$$

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{13}$$

We modeled the point-level intercepts as the outcome of a point-specific, canyon-level intercept ($\alpha_{k,s}$) and the product of an array of point-level slope parameters (β_{point}) and point-level predictors ($\boldsymbol{X}_{point}$, Table 1).

$$\alpha_{j,k,s} \sim Normal\left(\mu_{j,k,s}, \sigma_{k,s}\right), \tag{14}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}\boldsymbol{X}_{point}, \tag{15}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{16}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal\left(\mu_{k,s}, \sigma_s\right), \tag{17}$$

$$\mu_{k,s} = \alpha_s, \tag{18}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{19}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{20}$$

$$\mu_0 \sim Normal(0, 2), \tag{21}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{22}$$

Model fitting

We fitted models in R (v3.4.1, R Core Team 2017; Williamson 2019) with the rstan package (Stan Development Team 2018), a wrapper to the Hamiltonian Monte Carlo program Stan (Stan Development Team 2017). We used four sampling chains, each with 2000 iterations (1000 iterations for warmup), and set the adaptation parameter (adapt delta) to 0.95. The latter reduces the step-size of the sampler to allow sampling of complex posterior geometries of model parameters and reduces the potential that bias will result from chains that do not sample the posterior distribution effectively (Stan Development Team 2017).

Assessing model fit

We assessed goodness-of-fit of the occurrence model by evaluating the area under the receiver-operating curve [AUC; implemented in package pROC (Robin et al. 2011)]. AUC > 0.75 is regarded as a good model fit and AUC $\sim$ 1 as an excellent fit to the data. We evaluated the AUC for the lower quartile, median, and

upper quartile values for posterior predictions of p (the posterior estimate of the probability of occurrence) to evaluate the sensitivity of our AUC calculations across the posterior distribution of p.

For the binomial models, we sampled values from the posterior of the parameterized model ($y_{i,jk,s}^{sampled}$) and calculated the Freeman-Tukey measure of discrepancy for the observed ($y_{i,j,k,s}^{obs}$) or sampled data, given their fitted values ($\mu_{j,k,s}$):

$$D_{obs} = \sum_i \sqrt{\left(y_{i,j,k,s}^{obs} - \mu_{j,k,s}\right)^2}; \quad (23)$$

$$D_{sampled} = \sum_i \sqrt{\left(y_{i,j,k,s}^{sampled} - \mu_{j,k,s}\right)^2} \quad (24)$$

Any number of samples from the posterior can be drawn and corresponding discrepancies calculated. The posterior predictive fit is the proportion of sampled discrepancies that exceed the observed discrepancy. Values of posterior predictive fit near 0.5 indicate excellent model fits, but values from 0.05 through 0.95 are regarded as plausible fits of the parameterized model to the data (Gelman et al. 2013).

Strength of association of individual predictors

We assessed the strength of evidence that a predictor was strongly associated with the probability of occurrence (Bernoulli model) or with the prevalence (binomial model) of cheatgrass by calculating the proportion of the posterior probability distribution that exceeded zero for each predictor's regression coefficient. Predictors for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 were regarded, respectively, as strongly and positively or strongly and negatively associated with the response variable. Given our use of uninformative priors (i.e., half of the posterior predictive mass ≥ 0), posterior proportions > 0.90 correspond to odds ratios of > 10, which are strong positive associations (Jeffreys 1961). Similarly, posterior proportions < 0.10 equate to odds ratios of < 0.1, which are evidence of strong negative associations.

We did not interpret the strength of associations of predictors on the basis of the magnitudes of the regression coefficients for two reasons. First, only the continuous predictors were scaled given that the mean of a binary predictor is not relevant, making comparisons with the binary predictors inappropriate. Second, although expressing the continuous predictors on a common scale facilitates model fitting, it results in regression coefficients that indicate the predicted change in outcome associated with a unit standard deviation change in the predictor value. As such, the regression coefficients provide an estimate of the relative effect of the predictor subject to its measured variation and conditional on all other predictors in the model. Given that our continuous predictors had different standard deviations, use of the magnitude of the regression coefficients to compare the relative strength of the predictors in our models would be inappropriate. Instead, we provide marginal effects plots to illustrate the effect of multiple standard deviation changes in the predictor on the response while all other predictors are held at their mean.

Results

Occurrence models for all sample points and unburned points fitted the data well (AUC > 0.98 for the median, lower, and upper quartile posterior estimates of p). Posterior predictive checks indicated that the prevalence models also fitted the data well, with posterior predictive fits of 0.25, 0.32, and 0.26 for models that included all sample points, unburned points only, and burned points only, respectively.

The probabilities of cheatgrass occurrence and prevalence were associated strongly with fire. Results of the model that included all sample points (Fig. 2A) indicated that fire occurrence was associated with an increase in the probability of cheatgrass occurrence (Table 2, Fig. 2B) and an increase in prevalence (conditional on cheatgrass presence; Table 3, Fig. 2C). In models restricted to burned points, cheatgrass prevalence increased as time since fire increased. However, the strength and sign of the quadratic term suggested that this relation may peak at intermediate values of time since fire.

Grazing and prevalence of native perennial grasses were associated with the probability of cheatgrass occurrence and prevalence. Models that included either all sample points or only unburned points (Fig. 3A) indicated that grazing occurrence and an increase in the proportion of years grazed were associated positively with an increase in the

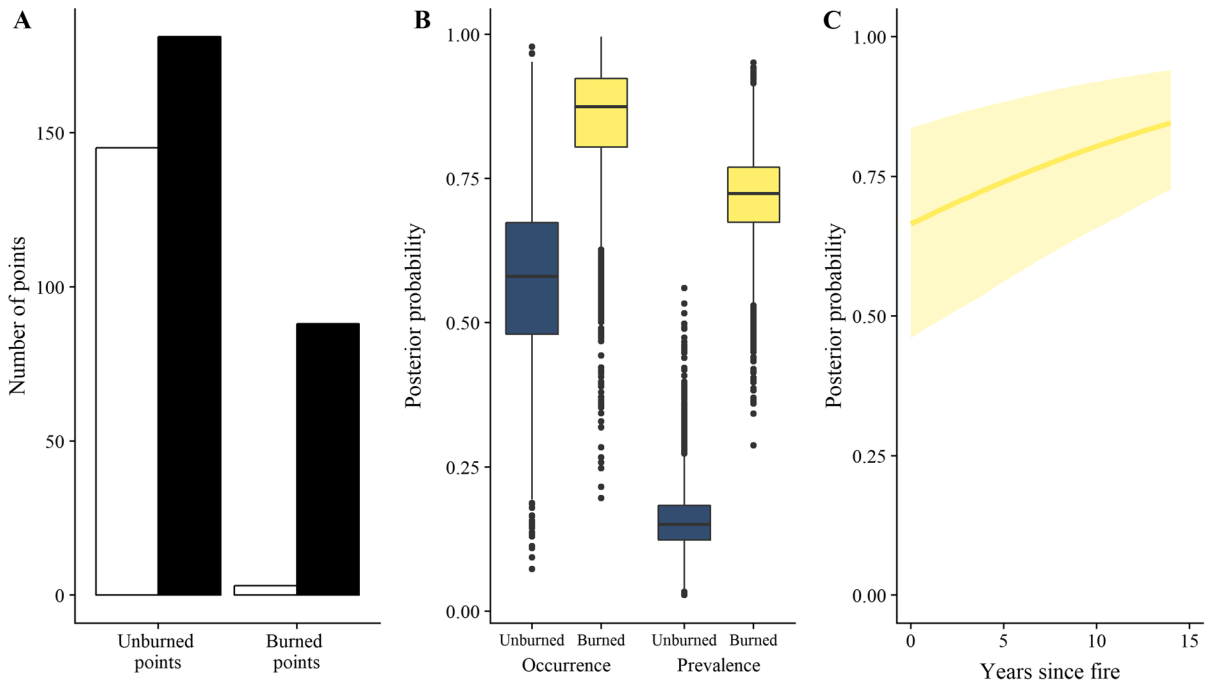


Fig. 2 Relations between fire and the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year). Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of sample points in which cheatgrass was recorded present (black) was much greater than the number of sample points in which it was recorded absent (white); cheatgrass was recorded present in 97% of burned points. **B** Probability of occurence of cheatgrass and of prevalence of cheatgrass were higher in models that included only burned points (yellow) than in models that included only unburned points (blue). **C** In the model restricted to burned points, the marginal effect of time since fire on cheatgrass prevalence (conditional on cheatgrass presence) was strongly positive. SD, standard deviation from the mean value of time since fire

Table 2 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of cheatgrass occurrence

Variable	All sample points Mean (SD)	Unburned points Mean (SD)
Elevation	− 0.46 (0.23)*	− 0.43 (0.24)*
Hillshade index	0.17 (0.15)	0.14 (0.17)
Median winter precipitation	− 0.07 (0.23)	− 0.02 (0.25)
Median proportion of precipitation falling in winter	− 0.47 (0.23)*	− 0.42 (0.25)*
Burned (yes/no)	1.64 (0.56)*	NA
Grazed (yes/no)	0.64 (0.44)*	0.25 (0.45)

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with occurrence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)

probability of cheatgrass occurrence (Table 2, Fig. 3B) and in the prevalence of cheatgrass (Table 3, Fig. 3C). However, in models restricted to burned points, prevalence of cheatgrass remained quite high, but decreased slightly as the proportion of years grazed increased (Table 3, Fig. 3D). Few burned points (8 of 91) were not grazed. In models that included all sample points or only unburned points,

Table 3 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Variable	All sample points Mean (SD)	Unburned points Mean (SD)	Burned points Mean (SD)
Elevation	0.03 (0.04)	0.09 (0.06)*	0.41 (0.10)*
Hillshade index	− 0.08 (0.02)*	− 0.13 (0.03)*	− 0.31 (0.03)*
Median spring precipitation over the study period	NA	NA	− 0.53 (0.09)*
Median winter precipitation over the study period	0.15 (0.03)*	0.04 (0.06)	0.25 (0.06)*
Median proportion of precipitation falling in winter over the study period	− 0.18 (0.04)*	0.01 (0.06)	0.04 (0.04)
Burned (yes/no)	2.69 (0.06)*	NA	NA
Time since fire	NA	NA	1.03 (0.05)*
Time since fire^2	NA	NA	− 0.73 (0.03)*
Proportion of years grazed	0.47 (0.03)*	0.13 (0.06)*	− 0.13 (0.04)*
Prevalence of perennial grasses	− 0.08 (0.03)*	− 0.18 (0.04)*	− 0.01 (0.03)
Spring precipitation in the year of observation	− 0.31 (0.08)*	0.00 (0.04)	− 0.22 (0.11)*
Winter precipitation in the year of observation	0.27 (0.07)*	NA	0.26 (0.09)*
Proportion of precipitation falling in winter in the year of observation	− 0.27 (0.07)*	− 0.16 (0.04)*	− 0.27 (0.11)*

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with prevalence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)

prevalence of cheatgrass decreased as prevalence of perennial grasses increased (Table 3). We did not estimate relations between prevalence of perennial grasses and probability of cheatgrass occurrence because we did not have a complete record of perennial grass prevalence and, therefore, could not estimate the median prevalence of perennial grasses across the study period.

The response of cheatgrass to longer-term precipitation (median winter and spring precipitation and the median proportion of precipitation falling in winter) was inconsistent. Median winter precipitation was not strongly associated with probability of cheatgrass occurrence (Table 2) but was associated positively with cheatgrass prevalence in models that included all sample points or only burned points (Fig. 4A). The median proportion of precipitation falling in winter was negatively associated with the probability of cheatgrass occurrence in models that included all sample points or only unburned points (Table 2, Fig. 4B). Similarly, the proportion of precipitation falling in winter in the year of observation was negatively associated with cheatgrass prevalence in all three models (Table 3, Fig. 4C). We did not include median spring precipitation as a predictor because it was highly correlated with median winter precipitation. However, regardless of the amount or proportion of winter precipitation, prevalence of cheatgrass in models restricted to burned points increased as median spring precipitation decreased.

Precipitation in the year of observation was associated strongly with the prevalence of cheatgrass. In models that included all sample points or only burned points, cheatgrass prevalence increased as winter precipitation increased (Table 3, Fig. 4C). The effect could not be estimated in the model restricted to unburned points, in which winter precipitation was excluded given its high correlation with other variables.

Elevation was associated strongly with cheatgrass occurrence in all models and with prevalence of cheatgrass in models restricted to unburned or burned points (Tables 2, 3; Fig. 5A). Probability of cheatgrass occurrence increased as elevation decreased, and prevalence increased as elevation increased when controlling for fire (i.e., restricting the data to either burned or unburned points, Tables 2, 3; Fig. 5B, C). This may be due to the occurrence of most fires at the lower end of the range of elevations occupied by cheatgrass. Solar exposure was not strongly associated with probability of cheatgrass occurrence (Table 2),

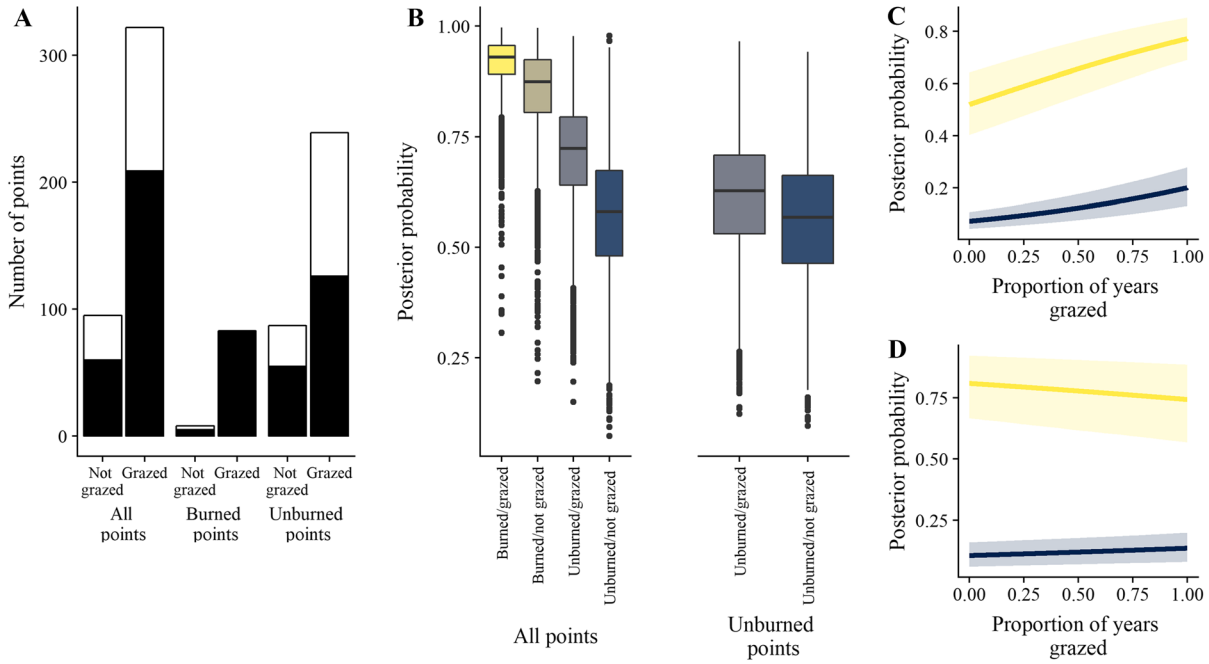


Fig. 3 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to the interaction between livestock grazing and fire. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Livestock grazing and fire both increased the probability of cheatgrass occurrence. Yellow, grazed and burned; tan, burned only; gray, grazed only; blue, neither grazed nor burned. Values derived from models that included either all sample points or unburned points. **C** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that included all sample points. Yellow, burned points; blue, unburned points. SD, standard deviation from the mean value of proportion of years grazed. **D** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that were restricted to either burned points (yellow) or unburned points (blue)

but prevalence increased as exposure decreased (Table 3).

Discussion

We capitalized on spatially and temporally extensive data on cheatgrass in both burned and unburned areas to evaluate explicitly the associations of fire, livestock grazing, precipitation, elevation, and solar exposure with probability of occurrence and with prevalence of cheatgrass across a large area and extensive topographic gradients. Our results generally were consistent with expectations that fire and a history of livestock grazing are associated positively with probability of cheatgrass presence and prevalence, and that ongoing disturbance is likely to induce expansion and increases in cover, density, abundance, or similar measures. Moreover, our work highlights that the potential response of cheatgrass to any one predictor, regardless of whether that predictor can be managed, is affected by other biotic and abiotic environmental attributes and feedbacks.

Regardless of fire history, cheatgrass was more likely to be recorded present at lower elevations. However, given presence, cheatgrass prevalence was greater at higher elevations and in areas with lower solar exposure. These areas likely have relatively high soil water availability while meeting the thermal requirements of cheatgrass for establishment, growth, and seed production (Chambers et al. 2007, 2016). Many of these areas are in canyons and occur in association with pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*, *J. occidentalis*) trees, which may reduce the exposure of cheatgrass to sunlight and heat stress. Higher prevalence of

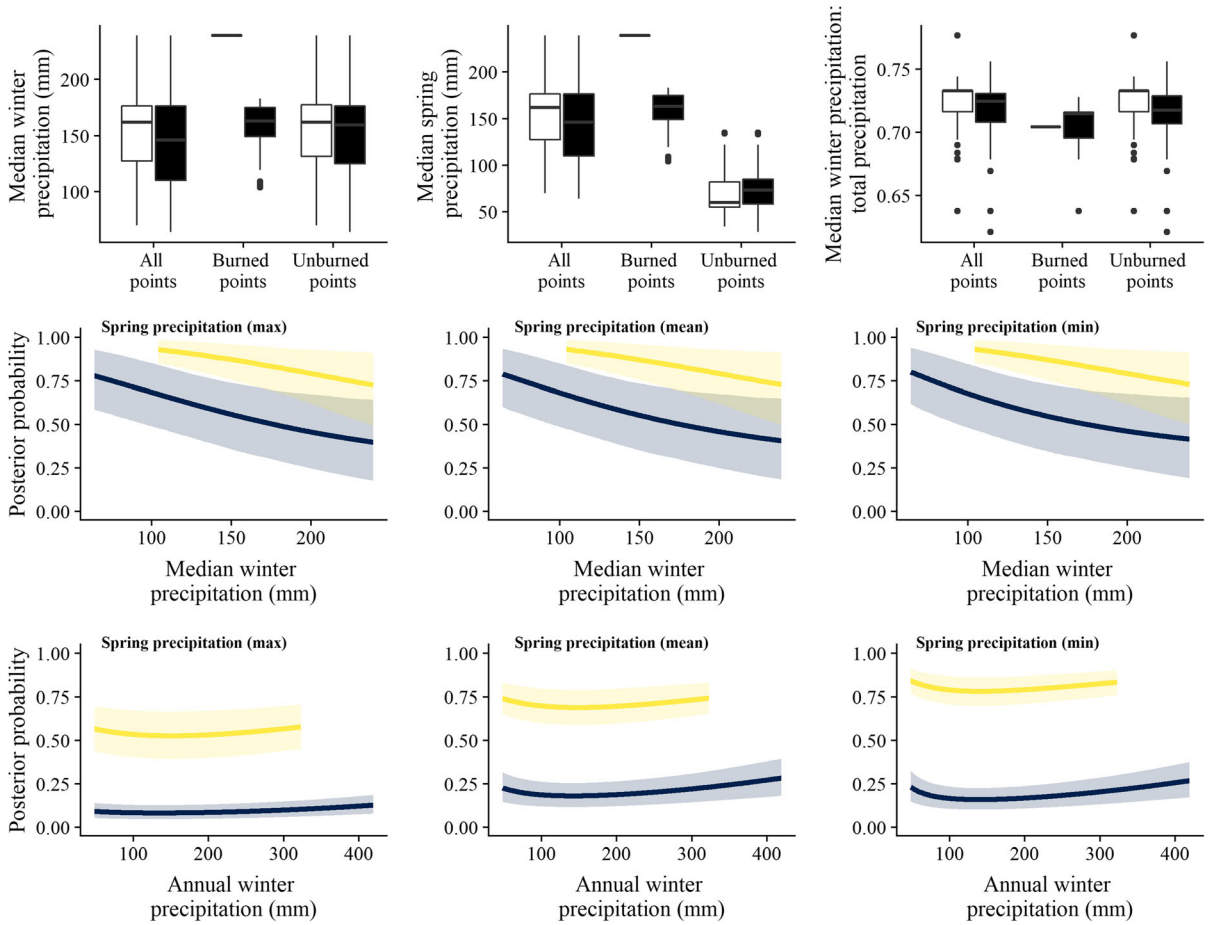


Fig. 4 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to precipitation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. Top row: Median winter precipitation, spring precipitation, or proportion of precipitation falling in winter at sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. Middle row: The probability of cheatgrass occurrence decreased as median winter precipitation (or the median proportion of precipitation falling in winter) increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. Yellow, burned points; blue; unburned points. SD, standard deviation from the mean value of median winter precipitation. Bottom row: The probability of cheatgrass prevalence increased as median winter precipitation (or the median proportion of precipitation falling in winter) over the study period increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. SD, standard deviation from the mean value of winter precipitation in the year of sampling

cheatgrass at relatively high elevations at the edges of unoccupied areas suggests that cheatgrass is likely to expand to higher elevations if thermal conditions are consistent with its requirements and if ground disturbances continue.

Consistent with previous studies on the cheatgrass-fire cycle (Balch et al. 2013; Germino et al. 2016; Bradley et al. 2018), the presence of fire was the predictor most strongly associated with probability of cheatgrass presence and was positively related to prevalence. In models restricted to burned points, prevalence of cheatgrass increased as time since burn increased. A lag in increases in cheatgrass density and cover of one to three years after fire is common (Chambers et al. 2016). Subsequent increases in cover and density can occur over time as the abundance of cheatgrass in the seed bank increases (Chambers et al. 2016).

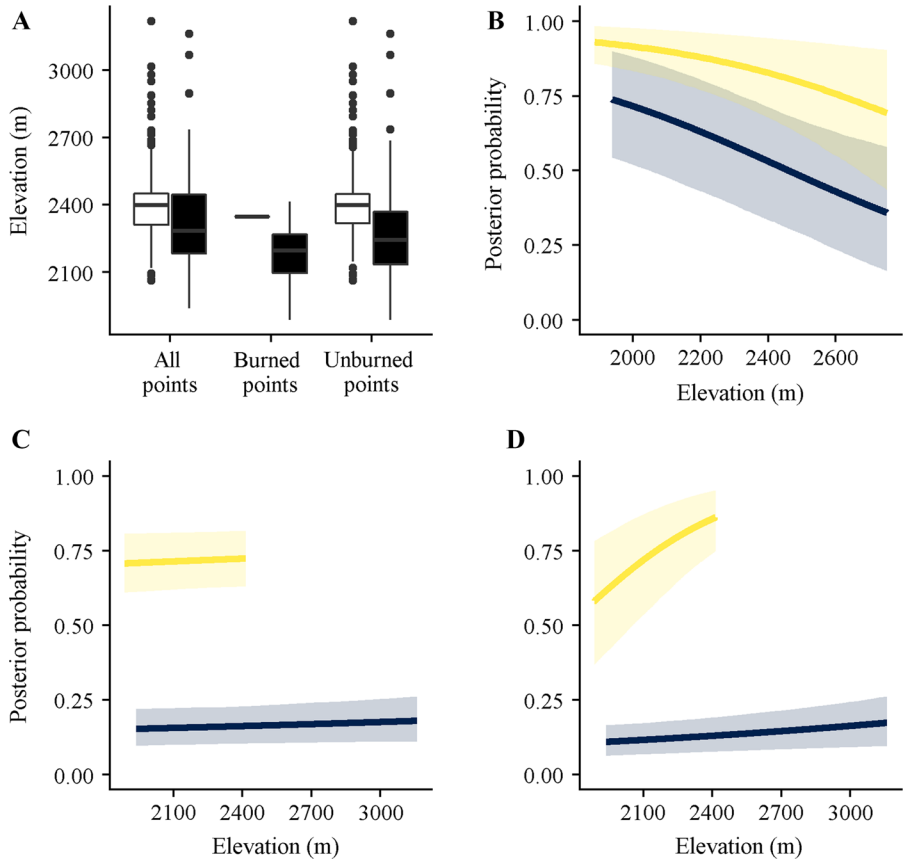


Fig. 5 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to elevation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** Elevational distribution of sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Probability of cheatgrass occurrrence decreased as elevation increased in a model that included all sample points (yellow, burned; blue, unburned). SD, standard deviation from the mean value of elevation. **C** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in a model that included all sample points. **D** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in models that were restricted to either burned points (yellow) or unburned points (blue). Differences in line lengths reflect different elevational ranges covered by the points included in the three models

Abundance of perennial native herbaceous species often is associated negatively with the abundance of cheatgrass or other non-native invasive annual grasses following prescribed fire and other management treatments (Davies 2008; Chambers et al. 2014). We found negative associations between prevalence of native perennial grasses and prevalence of cheatgrass in models that included all sample points or only unburned points, but not in models restricted to burned points. Following fire, loss of sagebrush and other fire-intolerant woody species increases the area of habitat for cheatgrass, soil water content, and nutrient content, and typically leads to increases in cheatgrass presence and abundance (Roundy et al. 2014, 2018). Cheatgrass likely will persist on these burned sites. However, maintaining or increasing the abundance of native perennial grasses can increase resistance to cheatgrass (Chambers et al. 2016; Pyke et al. 2016). The longer-term trajectories of these systems are unknown, but the strength and sign of the quadratic form of time-since-fire suggests that prevalence may stabilize or even decrease slightly at some point beyond the 14-year period we examined.

Consistent with Reisner et al. (2013), our analyses of all sample points and of only unburned points support the inference that, over an extensive area, both the presence of livestock grazing and the proportion of years in which a location is grazed are associated with an increase in the probability of presence and prevalence of cheatgrass. However, the negative association between the proportion of years grazed and prevalence of cheatgrass in models restricted to burned points may reflect a modest reduction in cheatgrass growth and seed production. This decrease in cheatgrass prevalence was accompanied by a decrease in the incidence of perennial grasses, suggesting that grazing on burned sites may lead to an overall decrease in herbaceous cover or biomass rather than selectively suppressing cheatgrass per se. Regardless, that the probability of encountering cheatgrass at any observation around a sample point (i.e., probability of prevalence) was > 0.5 on burned sites suggests that cheatgrass is likely to remain fairly dense on sites that are both burned and grazed, even if prevalence decreases modestly from its absolute peak.

It has been suggested that livestock grazing can reduce fuel loads and the likelihood of severe fires in sagebrush ecosystems (Davies et al. 2010). In the Owyhee Front in southern Idaho, the BLM has begun implementing intensive grazing in an effort to create fuel breaks, although evidence that fuel breaks reduce the spread and undesirable effects of fire is lacking (Shinneman et al. 2019). Grazing often reduces the abundance of perennial native grasses, which can facilitate increases in the presence and relative abundance of cheatgrass (Reisner et al. 2013, 2015); as our work suggests, these increases can occur over large areas, especially after fire. Widespread increases in cheatgrass presence and abundance, in turn, can increase fine-fuel loads and the likelihood of more frequent and extensive wildfires (Balch et al. 2013). We acknowledge that our characterization of grazing history includes some uncertainty. Grazing by cattle and sheep has occurred throughout our study region for well over a century, and likely for at least 75 years on allotments that were active during the study period, but reliable records are limited. Although we do not have precise information on number of livestock per unit area, duration of grazing, or intensity of grazing, livestock grazing long has been the single most widespread land use across the Intermountain West. Our results suggest a strong positive relation between the probability of presence and prevalence of cheatgrass and livestock grazing, particularly in unburned locations, where resistance to cheatgrass is greater than in burned locations.

Cheatgrass prevalence tended to be lower in years in which precipitation at a given point was high relative to that point's long-term median, but higher when regional winter precipitation was high and regional spring precipitation was at or below the median for the study period. This result is consistent with observations that growth and reproduction of cheatgrass occur earlier than that of many native shrubs and grasses (Peterson 2005). As a result, cheatgrass abundance may respond more strongly than abundance of native species to precipitation early in the water year. For example, at relatively low elevations, autumn precipitation may lead to germination and establishment of cheatgrass, provided the thermal requirements of cheatgrass are met (Roundy et al. 2018). By contrast, native species that compete with cheatgrass may respond more strongly than cheatgrass to precipitation later in the water year. Many of our observations of high prevalence of cheatgrass that coincided with relatively high proportions of precipitation in winter were associated with water-years in which precipitation was low. Thus, the amount of precipitation falling during periods favorable for cheatgrass establishment and growth may be more important than the total precipitation for the year (Bradley and Mustard 2006; Chambers et al. 2014; Jones et al. 2015).

The frequency of wet days in the Intermountain West is projected to decrease during the 21st century, whereas the amount of precipitation on wet days (Polade et al. 2014) and variability in precipitation are projected to increase (Dettinger et al. 2011; Gershunov et al. 2013; Kunkel et al. 2013). It is unclear how these projected changes will affect water availability, and how water availability may affect land uses, such as livestock grazing. Our results suggest that both the timing and amount of precipitation may affect the abundance of cheatgrass. Moreover, increases in temperature may lead to expansion of cheatgrass at higher elevations. We believe that interactions between land use and climate change will continue to affect the composition, structure, and function of ecosystems throughout the arid western United States and globally. Our work may inform prioritization of management actions to minimize anthropogenic

drivers of climate change that independently and cumulatively drive expansion of cheatgrass, changes in fire cycles, and the status of species and ecosystems across the Intermountain West. Our results, which derive from a novel time-series of data on cheatgrass and covariates from within an extensive area, do not support the use of livestock grazing to suppress cheatgrass and its undesirable effects on the habitats of native species or regional fire dynamics. Livestock grazing with the aim of suppressing cheatgrass may be especially counterproductive in unburned areas in which native perennial grasses may remain viable.

Acknowledgements This research was supported by the Joint Fire Science Program (05-2-1-94, 09-1-08-4, and 15-1-03-6), the US National Science Foundation Graduate Research Fellowship Program (1650042), the US Geological Survey's Northwest and Southwest Climate Science Centers (F16AC00025), and the Strategic Environmental Research and Development Program of the US Department of Defense (RC-2202).

References

Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK (2005) Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. Ecol Appl 15:774–792

Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biol 19:173–183

Banks ER, Baker WL (2011) Scale and pattern of cheatgrass (*Bromus tectorum*) invasion in Rocky Mountain National Park. Nat Area J 31:377–390

Blackard JA, Dean DJ (1999) Comparative accuracies of artificial neural networks and discriminant analysis in predicting forest cover types from cartographic variables. Comput Electron Agric 24:131–151

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecol Appl 16:1132–1147

Bradley BA, Curtis CA, Chambers JC (2016) *Bromus* response to climate and projected changes with climate change. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zürich, pp 257–274

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu MN (2018) Cheatgrass (*Bromus tectorum*) distribution in the Intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biol Invasions 20:1493–1506

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM et al (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brooks ML, Brown CS, Chambers JC, D'Antonio CM, Keeley JE, Belnap J (2016) Exotic annual *Bromus* invasions: comparisons among species and ecoregions in the western United States. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zürich, pp 11–60

Brummer TJ, Taylor KT, Rotella JJ, Maxwell BD, Rew LJ, Lavin M (2016) Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. Ecosystems 19:986–1000

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

Chambers JC, Board D, Dhaemers J, Reiner A (2010) Vegetation response to prescribed fire in the Shoshone mountains of Nevada. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2010-0016

Chambers JC, Miller RF, Board DI, Grace JB, Pyke DA, Roundy BA, Schupp EW, Tausch RJ (2014) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangel Ecol Manag 67:440–454

Chambers JC, Germino MJ, Belnap J, Brown CS, Schupp EW, St. Clair SB (2016) Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zurich, pp 275–306

Chambers JC, Maestas JD, Pyke DA, Boyd C, Pellant M, Wuenschel A (2017) Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and Greater sage-grouse. Rangel Ecol Manag 70:149–164

Compagnoni A, Adler PB (2014) Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. Ecosphere 5(9):121. https://doi.org/10.1890/ES14-00047.1

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Davies KW (2008) Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangel Ecol Manag 61:110–115

Davies KW, Bates JD, Svejcar TJ, Boyd CS (2010) Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. Rangel Ecol Manag 63:662–669

Davies GM, Bakker JD, Dettweiler-Robinson E, Dunwiddie P, Hall SA, Downs J, Evans J (2012) Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. Ecol Appl 22:1562–1577

Dettinger MD, Ralph FM, Das T, Neiman PJ, Cayan DR (2011) Atmospheric rivers, floods and the water resources of California. Water 3:445–478

Fleishman E (2015) Vegetation structure and composition in the Shoshone Mountains and Toiyabe, Toquima, and Monitor ranges, Nevada, 2nd edn. Forest Service Research Data Archive, Fort Collins. https://doi.org/10.2737/RDS-2013-0007-2

Freeman ED, Sharp TR, Larsen RT, Knight RN, Slater SJ, McMillan BR (2014) Negative effects of an exotic grass invasion on small-mammal communities. PLoS ONE 9(9):e108843. https://doi.org/10.1371/journal.pone.0108843

Garton EO, Connelly JW, Horne JS, Hagen CA, Moser A, Schroeder MA (2011) Greater Sage-Grouse population dynamics and probability of persistence. In: Knick ST, Connelly JW (eds) Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, vol 38. University of California Press, Berkeley, pp 293–381

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv Biol 17:420–432

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis, 3rd edn. CRC Press, Boca Raton

Germino MJ, Belnap J, Stark JM, Allen EB, Rau BM (2016) Ecosystem impacts of exotic annual invaders in the genus *Bromus*. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, New York, pp 11–60

Gershunov A et al (2013) Future climate: projected extremes. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds) Assessment of climate change in the southwest United States: a report prepared for the National Climate Assessment. Island Press, Washington, DC, pp 126–147

Jeffreys H (1961) Theory of probability, 3rd edn. Clarendon Press, Oxford

Jones RO, Chambers JC, Board DI, Johnson DW, Blank RR (2015) The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (*Bromus tectorum*). Ecosphere 6(7):107. https://doi.org/10.1890/ES14-00285.1

Knapp PA (1998) Spatio-temporal patterns of large grassland fires in the Intermountain West, USA. Global Ecol Biogeogr 7:259–272

Kunkel KE, Karl TR, Easterling DR, Redmond K, Young J, Yin X, Hennon P (2013) Probable maximum precipitation and climate change. Geophys Res Lett 40:1402–1408

Larson CD, Lenhoff EA, Rew LJ (2017) A warmer and drier climate in the northern sagebrush biome does not promote cheatgrass invasion or change its response to fire. Oecologia 185:763–774

Mack RN (1981) Invasions of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hooved mammals. Am Nat 119:757–773

Meyer SE, Garvin SC, Beckstead J (2001) Factors mediating cheatgrass invasion of intact salt desert shrubland. In: McArthur ED, Fairbanks DJ (compilers) Proceedings—Shrubland Ecosystem Genetics and Biodiversity; 13–15 June 2000. RMRS-P-21, US Department of Agriculture Forest Service, Rocky Mountain Research Station, Provo, Utah

Miller RF, Chambers JC, Pyke DA, Pierson FB, Williams CJ (2013) A review of fire effects on vegetation and soils in the Great Basin region: response and ecological site characteristics. General Technical Report RMRS-GTR-308, US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado

Mullahy J (1986) Specification and testing of some modified count data models. J Econom 33:341–365

NOAA National Centers for Environmental Information (NCEI) (2018) U.S. billion-dollar weather and climate disasters. https://www.ncdc.noaa.gov/billions/

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Karieva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Peterson EB (2005) Estimating cover of an invasive grass (*Bromus tectorum*) using tobit regression and phenology derived from two dates of Landsat ETM plus data. Int J Remote Sens 26:2491–2507

Pilliod DS, Welty JL, Arkle RS (2017) Refining the cheatgrass-fire cycle in the Great Basin: precipitation and fine fuel composition predict wildfire trends. Ecol Evol 7:8126–8151

Polade SD, Pierce DW, Cayan DR, Gershunov A, Dettinger MD (2014) The key role of dry days in changing regional climate and precipitation regimes. Nat Sci Rep 4:4364. https://doi.org/10.1038/srep04364

Pyke DA, Chambers JC, Beck JL, Brooks ML, Mealor BA (2016) Land uses, fire and invasion: exotic annual *Bromus* and human dimensions. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Zurich, pp 307–337

Reisner MD, Grace JB, Pyke DA, Doescher PS (2013) Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. J Appl Ecol 50:1039–1049

Reisner MD, Doescher PS, Pyke DA (2015) Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. J Veg Sci 26:1212–1224

Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez J, Müller M (2011) pROC: an open-source package for R and S + to analyze and compare ROC curves. BMC Bioinform 12:77. https://doi.org/10.1186/1471-2105-12-77

Roundy BA, Young K, Cline N, Hulet A, Miller RR, Tausch RJ, Chambers JC, Rau B (2014) Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangel Ecol Manag 67:495–505

Roundy BA, Chambers JC, Pyke DA, Miller RF, Tausch RJ, Schupp EW et al (2018) Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. Ecosphere 9:02417

Shinneman DJ, Germino MJ, Piliod DS, Aldridge CL, Vaillant NM, Coates PS (2019) The ecological uncertainty of wildfire fuel breaks: examples from the sagebrush steppe. Front Ecol Environ. https://doi.org/10.1002/fee.2045

Stan Development Team (2017) Stan modeling language: user's guide and reference manual. Version 2.17.0

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3. http://mc-stan.org/

Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L (2017) Challenges and limitations to native species restoration in the Great Basin, USA. Plant Ecol 218:81–94

Taylor K, Brummer T, Rew LJ, Lavin M, Maxwell BD (2014) *Bromus tectorum* response to fire varies with climate conditions. Ecosystems 17:960–973

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Urza A, Weisberg PJ, Chambers JC, Board DI, Dhaemers J, Flake S (2017) Post-fire vegetation response at the woodland-shrubland interface is mediated by the pre-fire community. Ecosphere 8(6):e01851. https://doi.org/10.1002/ecs2.1851

US Department of the Interior Bureau of Land Management (BLM) (2007) Burned area emergency stabilization and rehabilitation handbook. BLM Handbook H-1742-1. https://www.blm.gov/sites/blm.gov/files/uploads/Media_Library_BLM_Policy_Handbook_h1742-1.pdf

U.S. Fish and Wildlife Service (USFWS) (2015) Endangered and threatened wildlife and plants; 12-month finding on a petition to list the greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species; proposed rule. Fed. Register 80, 59858–59942. http://www.gpo.gov/fdsys/pkg/FR-2015-10-02/pdf/2015-24292.pdf. Accessed 9 Jan 2016

Williamson, MA (2019) Code for Williamson et al. 2019. https://doi.org/10.5281/zenodo.3237935. Available at https://github.com/mattwilliamson13/GBbrte

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.