

Appendix A for the Objection filed against the Dixie National Forest Prescribed Fire Landscape Resiliency Project by NEC, AWR, Y2U and CBD on October 10, 2023.

Appendix A contains relevant portions of cited literature and/or reports, including:

Baker, W., 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177-185.

Baker, W., and D. Shinneman. 2004. Fire and restoration of pinon-juniper woodlands in the western United States: a review. Forest Ecology and Management 189:1-21.

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Fire and Restoration of Sagebrush Ecosystems

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Abstract

Wildlife managers often resort to prescribed fire to restore sagebrush (*Artemisia* spp.) ecosystems thought to have been affected by fire exclusion. However, a fire mosaic of burned and unburned areas may be tolerated by certain wildlife but can be detrimental to sagebrush obligates. This article assesses evidence about the historical frequency and pattern of fire in sagebrush ecosystems and the need for prescribed fire. Fire-scar data from nearby forests require adjustment to estimate fire rotation, the time required to burn once through a sagebrush landscape. Estimates from forests require correction for unburned area and because sagebrush burns less often than forests. Recovery time also might indicate fire rotation. Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) recovers within about 35–100 or more years after fire, and Wyoming big sagebrush (*A. t. ssp. wyomingensis*) requires 50–120 or more years. Fire rotation in other ecosystems is 2 or more times the recovery period. Together, the evidence suggests fire rotations may be a minimum of 325–450 years in low sagebrush (*A. arbuscula*), 100–240 years in Wyoming big sagebrush, 70–200 years or more in mountain big sagebrush, and 35–100 years in mountain grasslands with a little sagebrush. Given these long rotations, fire exclusion likely has had little effect in most sagebrush areas. If maintaining and restoring habitat for sagebrush-dependent species is the goal, fire should be suppressed where there is a threat of cheatgrass (*Bromus tectorum*). Elsewhere, fire does not need to be reintroduced until native understory plants can be restored, so that sagebrush ecosystems can fully recover from fire. (WILDLIFE SOCIETY BULLETIN 34(1):177–185; 2006)

Key words

Artemisia spp., fire history, fire rotation, prescribed fire, sagebrush.

Sagebrush (*Artemisia* spp.) ecosystems and the species dependent upon them are under threat in western North America (Knick et al. 2003). Sagebrush has been viewed as a pest and eradicated using fire and other means but also has been converted to agriculture, overgrazed by domestic livestock, and invaded by non-native plants (Vale 1974, Knick and Rotenberry 1997, Knick et al. 2003). In this context, fire may be a double-edged sword in perpetuating and restoring sagebrush landscapes and their associated wildlife. Invasion by cheatgrass (*Bromus tectorum*) has led to a grass-fire cycle in which increasing cheatgrass promotes large fires that allow cheatgrass to increase further, eroding and fragmenting remaining stands of sagebrush (Whisenant 1990, Knick and Rotenberry 1997, Knick 1999). Fire also may have been reduced or excluded in some areas due to loss of fine fuels to overuse by livestock, landscape fragmentation, and intentional fire suppression (Wroblewski and Kauffman 2003). Are sagebrush landscapes suffering from too much fire or too little? Should fire be suppressed or restored? Answers to these questions depend on the situation but also on our understanding of the historical role of fire before EuroAmerican settlement.

How fire is managed may have significant implications for wildlife, as a mosaic of burned and unburned areas is characteristic of modern sagebrush fires, and the pattern and extent of patchiness influences wildlife. Small prescribed fires may directly decrease habitat for sagebrush obligates, such as Brewer's sparrows (*Spizella breweri*) and sage thrashers (*Oreoscoptes montanus*) (Castrale 1982, Kerley and Anderson 1995). At the landscape scale, the fire mosaic may have adverse impacts if unburned areas are too small, as these birds are favored by large, unfragmented sagebrush areas (Kerley and Anderson 1995, Knick and Rotenberry 1995). However, if unburned areas are large, these birds may be little affected (Petersen and Best 1987).

Earlier studies suggested that sage-grouse (*Centrocercus* spp.)

might be favored by a burn mosaic (Klebenow 1973). However, sage-grouse may be adversely affected by a landscape mosaic of adjacent young burns, as these burns may all lack good nesting habitat (Nelle et al. 2000) and do not meet the habitat requirements of sage-grouse at other seasons (Wambolt et al. 2002). Brood-rearing habitat for sage-grouse may not be enhanced by fire in xeric sagebrush areas, even if a mosaic is created, as forbs and insects may not increase (Fischer et al. 1996). Overall, small infrequent fires may have a slight positive effect, but large, frequent fires (e.g., every 17 years) can cause extinction of grouse populations (Pedersen et al. 2003).

Similarly, generalist small mammals (e.g., deer mice [*Peromyscus maniculatus*]) are not adversely affected by either a patchy spring fire or an extensive stand-replacing autumn fire, but more specialized small mammals (e.g., jumping mice [*Zapus princeps*]) cannot survive extensive stand-replacing fires (McGee 1982). Regeneration of sagebrush after fire is probably enhanced by dispersal of seed from unburned plants (Wroblewski 1999, McDowell 2000, Longland and Bateman 2002). When all sagebrush plants are burned, recovery is very slow, as seed does not spread far from mature plants (Welch and Criddle 2003). Thus, large fires that lead to extensive loss of sagebrush cover may have negative effects on sagebrush obligate and more specialized species and may delay sagebrush recovery after fire (Longland and Bateman 2002).

Given these effects, have sagebrush ecosystems actually been affected by fire exclusion or an increase in fire? Winward (1991) suggested that most sagebrush stands were ≥ 60 years of age, which he thought implied that fire intervals have lengthened. Wroblewski and Kauffman (2003) suggested that fire suppression and overgrazing by livestock have lengthened fire intervals, leading to increased dominance of sagebrush. Junipers (*Juniperus* spp.), pinyons (e.g., *Pinus edulis*, *P. monophylla*), and Douglas-fir (*Pseudotsuga menziesii*) are thought to have invaded former

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sagebrush areas due to fire exclusion (Arno and Gruell 1983, Miller and Rose 1999).

Fire likely has increased in sagebrush areas where cheatgrass has become common. Wildfires in former sagebrush areas now dominated by cheatgrass are burning at short fire rotations. Fire rotation is the time required to burn once through an area, equal to the size of a particular study area (Baker and Ehle 2001). About 26% of cheatgrass-dominated lands in the Salt Lake District of the Bureau of Land Management burned in 11 years (Roberts 1990), a fire rotation of 42 years. Fires burned 45% of the Snake River Birds of Prey Area in southern Idaho over a 7-year period, where over 50% of this landscape is dominated by cheatgrass, leading to a fire rotation of about 15.5 years (Pellant 1990). Former sagebrush areas now dominated by cheatgrass may have a fire rotation too short to allow re-establishment of sagebrush (Whisenant 1990). Large, high-intensity cheatgrass fires leave fewer and smaller unburned patches of sagebrush, that are especially vulnerable to further cheatgrass invasion (Whisenant 1990, Knick and Rotenberry 1997).

Threats to the sagebrush ecosystem and the declining status of sage-grouse and other species have led to interest in ecosystem restoration. Some restoration proposals call for use of prescribed fire, others suggest it is better to suppress fires, especially where cheatgrass is a threat (Hemstrom et al. 2002, Bunting et al. 2003). Moreover, there are competing ideas about how often fire historically burned these ecosystems (Winward 1991, Welch and Criddle 2003), and there is little understanding of the pattern produced by natural fires in sagebrush landscapes. Also, standard measures of fire frequency do not provide estimates of the rate at which fire burned across landscapes, and a reassessment is warranted (Baker and Ehle 2001).

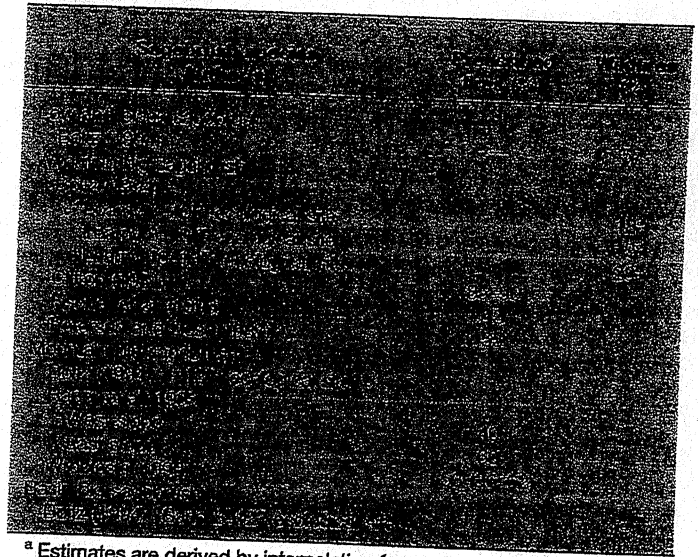
The purpose of this article is to review and reassess evidence about fire history, fire rotation, and the pattern of fire across sagebrush landscapes and from this evidence suggest the most promising directions for restoration. Sagebrush taxa that have been the subject of fire-history research include mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), and low sagebrush (*A. arbuscula*).

Fire Intensity and the Fire Mosaic

Fire intensity in sagebrush in the modern era has varied over a 7-fold range due to variation in fuel loads, shrub density, fuel moisture, wind speed, and other factors (Sapsis and Kauffmann 1991, Pyle and Crawford 1996). Low fire intensity, however, does not usually increase sagebrush survival; when flames reach sagebrush, mortality is nearly complete and the fire is "stand-replacing" (e.g., Blaisdell 1953, Britton and Clark 1985, Acker 1988, Sapsis and Kauffmann 1991). Britton and Clark (1985:23) report: "it is relatively unimportant how fast the fire moves, how hot the fire is, or what the fire intensity is... if a fire front passes through an area, the sagebrush will be killed." However, silver sagebrush (*A. cana*) and three-tip sagebrush (*A. tripartita*) may be killed, but often will re-sprout (White and Currie 1983, Shariff 1988).

Fires, thus, do not thin sagebrush stands or lower their density by killing a certain fraction of sagebrush throughout a stand as was implied in the past (Winward 1991). Fire exclusion cannot be a

Table 1. Percentage of area that is unburned within a fire perimeter in sagebrush. Studies reviewed include all studies conducted in North American over the last century.



* Estimates are derived by interpolating from a bar graph (Boltz 1994, fig. 2). Numerical ranges for Boltz's ecological sites are annual precipitation. Ecological sites that now contain significant cheatgrass and, thus, have less unburned area are omitted (e.g., "Loamy 10-12").

cause of increased density in a particular patch of existing sagebrush (Wroblewski and Kauffman 2003), brought on by an absence of thinning fires, as thinning fires did not occur.

Fire instead creates and controls the pattern and extent of a mosaic of burned and unburned areas. Unburned areas can result from 1) low sagebrush cover, 2) insufficient loading of fine fuels, 3) high fuel moisture, and 4) variable winds. A minimum of about 20% sagebrush cover and 300 kg/ha of herbaceous fuel might be required to carry fire in sagebrush (Britton and Clark 1985), but wind speed can significantly affect the fuel requirement (Brown 1982). Nonetheless, areas with low sagebrush density or little fine fuel can have mosaic burns (Ralphs and Busby 1979, Wright et al. 1979, Smith and Busby 1981). Lower fine-fuel production during droughts also may contribute to patchy burns (Hosten 1995, West and Yorks 2002). More unburned area also is common in cooler or moister parts of landscapes or during cooler or wetter conditions, as in early spring (Clifton 1981, Kuntz 1982, Boltz 1994, Colket 2003). Warmer, drier conditions, unless these reduce fine-fuel production, may lead to nearly complete sagebrush mortality and few or no islands of unburned sagebrush (Kuntz 1982, McGee 1982).

It is, thus, logical to suspect that pre-EuroAmerican fires in sagebrush landscapes left less unburned area in a mosaic, than is observed in modern prescribed fires (Wroblewski and Kauffman 2003), due to higher fine-fuel amounts, greater fuel continuity, and drier burning conditions. Modern fires often are burning through sagebrush that has reduced fine fuels due to overuse by domestic livestock. Today's summer wildfires seem to have less unburned area than do spring and autumn-prescribed fires, supporting the idea that hotter summer fires in the pre-EuroAmerican era would have left less unburned area (Table 1). Unfortunately, nothing is known directly about the extent and pattern of a fire mosaic in sagebrush in the pre-EuroAmerican era.

yr could maintain a sagebrush-bunchgrass community free of juniper. The data in Table 1 indicate that fires were probably more frequent than this." Given a 2.0 correction for forest adjacency and using Boltz's (1994) estimate of 21% unburned area, the fire rotation on mountain big sagebrush sites might have been somewhat less than 75–100 years. Waichler et al. (2001) has been cited (Crawford et al. 2004) as providing data suggesting mean CFI >200 years in xeric mountain big sagebrush on sandy soil in eastern Oregon. These data could not be located in Waichler et al. (2001), but these estimates, after correction for adjacency and unburned area, suggest the fire rotation in some mountain big sagebrush areas could be much longer than 75–100 years, perhaps several hundred years.

Past summaries of mean CFI in sagebrush did not recognize the limitations of these data and need for corrections to estimate fire rotation. Many summaries suggest that fires burned in some or even many mountain big sagebrush stands at intervals of 10 to somewhat less than 40 years (Winward 1985, 1991; Whisenant 1990, Miller 2002, United States Department of Interior 2002, Crawford et al. 2004), not recognizing that these short intervals are uncorrected mean CFI estimates for sites that were primarily grasslands, not sagebrush, in the pre-EuroAmerican era. Other summaries (Pellant 1990, Whisenant 1990) have used the "adjusted interval" of 32–70 years from table 1 in Houston's (1973) study, but this is also an uncorrected estimate from areas that were predominantly grasslands in the pre-EuroAmerican era. Summaries of mean fire interval for Wyoming big sagebrush have included 50 or 60 years on the low end (e.g., Miller 2002, United States Department of Interior 2002) or even 12–50 years for some stands (Miller 2002). However, there are no scar-based studies that support these short intervals. Moreover, all these intervals require correction for adjacency and unburned area and, once corrected, would still be low estimates, due to targeted sampling.

Evidence of Fire Rotation from Sagebrush Recovery Rate

The rate that sagebrush returns following fire is thought to be an indicator of fire frequency (Wright and Bailey 1982) and might also be used to estimate the fire rotation. Estimates of recovery time come from analysis of chronosequences of stands varying in time since fire (Fig. 1). Sagebrush density data are shown (Fig. 1), where cover data were not reported, but density is an insufficient measure of recovery, as it only indicates that shrubs are present, not that they are mature and have cover comparable to that in unburned control areas. Livestock grazing may hasten sagebrush recovery after fire (Pechanec and Stewart 1944), and more intense wildfires may decrease recovery, sometimes leading to fewer post-fire seedlings (Blaisdell 1953, Champlin 1983, Martin 1990). Unfortunately, there are insufficient data to allow analysis of the effects of these factors on sagebrush recovery rates.

In 2 studies, mountain big sagebrush recovered within about 35 years after fire to the same cover as sagebrush in unburned control areas (Fig. 1a). Welch and Criddle (2003) projected it would require 70 years or more just to get mountain big sagebrush back into the interior of a burn in Idaho, which is not recovery to full density, much less full cover. Perhaps a reasonable low estimate,

then, is 35–100 years or more for recovery of mountain big sagebrush.

For Wyoming big sagebrush, the required recovery period is less certain, as available data are meager after about 20 years of recovery (Fig. 1b). Very little recovery within the first 20 years is generally consistent among studies (Fig. 1b). The Wisdom sites in southwestern Montana (Walhof 1997, Wambolt et al. 2001) are exceptional, as they averaged about 96% recovery of cover 9 years after fire. Walhof (1997:60) reported: "These 2 sites may be atypical, and their responses are clearly not similar to other published data ..." Watts and Wambolt (1996) documented recovery to 76% of control area cover within 30 years, consistent with 72% recovery after 32 years at their Exlosure site in southwestern Montana (Walhof 1997, Wambolt et al. 2001). However, Colket (2003) found that, in southeastern Idaho, only 3 of 17 plots had recovered fully in density within 53 years, while full density recovery had been reached by 92 years on 16 of 17 plots. Colket (2003:58) reported that "... well over 53 years are required for big sagebrush to return to its pre-fire abundance." Another few decades beyond density recovery may be required for plants to mature and cover values to recover. Together these limited data suggest that full recovery of Wyoming big sagebrush may be quite variable but generally requires 50–120 or more years. In exceptional cases, recovery may occur within a decade (e.g., Wisdom sites).

The relationship between recovery period and fire rotation in other vegetation types suggests that fire rotation may be a multiple of the recovery period. In pinyon-juniper woodlands, for example, where documented fire rotations are 400–480 years (Baker and Shinneman 2004), the time to recover to a mature, closed-canopy condition is about 200 years (Tress and Klopatek 1987, Mehl 1992, Goodrich and Barber 1999), about half the fire rotation. Similarly, in lodgepole pine (*Pinus contorta*) and spruce-fir (*Picea-Abies*) forests, where fire rotations are about 300 years (Buechling and Baker 2004), a closed-canopy mature condition is reached in about 150 years, also about half the fire rotation (Despain and Romme 1991). Interior chaparral in southern California recovers within 20–30 years after fire, but fire rotations prior to about 1950, when fire regimes were less influenced by people, averaged about 80 years among nine counties (Keeley et al. 1999). These comparisons suggest the fire rotation may be twice or more the recovery period. Thus, fire rotations would be 70–200 years or more in mountain big sagebrush and 100–240 years or more in Wyoming big sagebrush. These estimates, which are imprecise, are at least similar in magnitude to scar-based estimates.

Conclusions

Combining the fire-scar and recovery evidence, the best available estimates of fire rotation are 325–450 years in low sagebrush, 100–240 years in Wyoming big sagebrush, 70–200 years or more in mountain big sagebrush, and 35–100 years in mountain grasslands where sagebrush is a minor component. These estimates are likely low estimates because they could not be corrected for targeted sampling and they use a conservative estimate of adjacency correction, but fire rotation in sagebrush cannot be estimated more precisely at this time using available data.

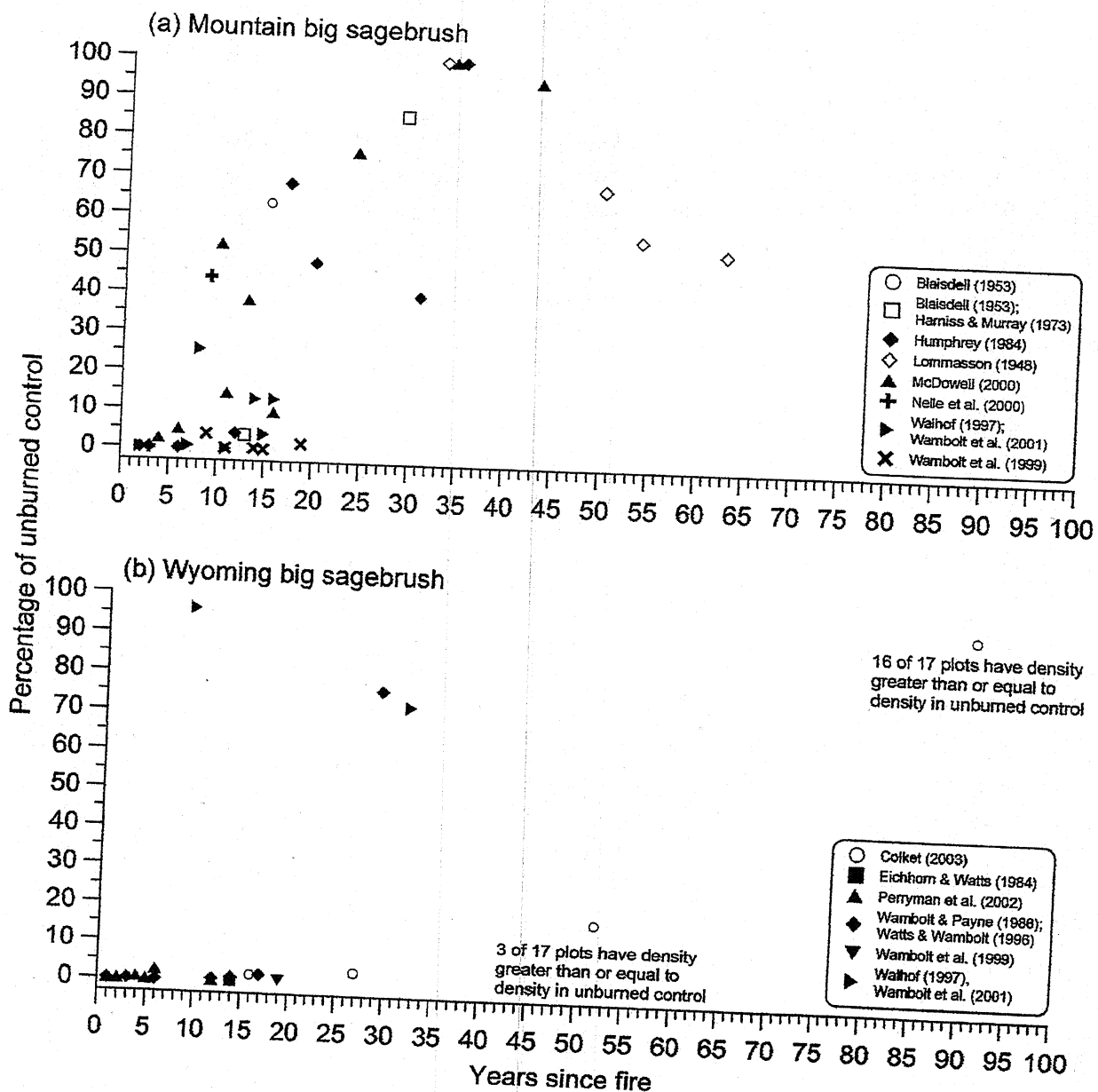


Figure 1. Sagebrush abundance versus time since fire, relative to unburned control areas, for (a) mountain big sagebrush and (b) Wyoming big sagebrush. These graphs include different measures of sagebrush abundance—density is shown as open symbols, cover as closed symbols. When authors did not specify the abundance in an unburned control area, the percentage is of the maximum value during the period covered by the study. When more than one value was reported for a particular time since fire, the mean was used. Many other studies that report recovery only within the first 10 years after fire (e.g., Pechanec and Stewart 1944, Acker 1988) are omitted. Lommasson (1948) does not identify the subspecies of big sagebrush, but it was likely mountain big sagebrush, based on the high elevation of the site. Studies reviewed include all studies conducted in North America over the last century.

Sagebrush has been assumed by some to be a fire-dependent vegetation type, requiring periodic renewal by fire (Winward 1991), although evidence challenging this fire dependence has been presented (Connelly et al. 2000, Welch and Criddle 2003). Fire is an important natural disturbance in sagebrush but does not occur as often as suggested in the past and is only one of many agents. Sagebrush density and cover are also diminished by droughts, insect outbreaks, and competition with native bunchgrasses, and may increase again during wet periods (Lommasson

1948, Maier et al. 2001, Anderson and Inouye 2001, Welch and Criddle 2003).

Given the long rotations that characterized pre-EuroAmerican fires in sagebrush, fire exclusion likely has had little effect in most sagebrush communities. A national assessment of fire regimes and fire-related condition classes (Schmidt et al. 2002) placed sagebrush mostly within fire regime II (stand replacement at 0–35-year frequency) and fire regime III (mixed severity at 35–100-year frequency). The source of these estimates is not documented,

but they are interpreted to mean that sagebrush has commonly missed several fires since EuroAmerican settlement and, thus, requires prescribed burning for restoration. However, the evidence presented here shows that these fire regimes underestimate the fire rotation, and there is no evidence of mixed-severity fire in sagebrush. Sagebrush instead generally belongs in fire regime V (long rotation, stand replacement). Where cheatgrass now dominates, sagebrush is likely in condition class 3 (fire regimes significantly altered from historical range), with too much fire. Sagebrush that has not entered a cheatgrass-fire cycle should remain in condition class 1 (fire regimes within historical range), not having missed much, if any, fire at this point. Similarly, the invasion of junipers, pinyons, and Douglas-fir into sagebrush areas (Arno and Gruell 1983, Miller and Rose 1999) is likely not generally due to fire exclusion, but to other factors (e.g., overgrazing).

Particularly in Wyoming big sagebrush, a program of prescribed burning is unwarranted or inadvisable if maintaining and restoring sagebrush landscapes and sagebrush-dependent species is the goal. Correcting for fire exclusion by reintroducing fire is likely not a common sagebrush restoration need. Also, little is known about the pattern of a mosaic created by pre-EuroAmerican fires or the importance of particular aspects of this mosaic to viability of wildlife populations (Longland and Bateman 2002). There is, thus, insufficient basis for prescribed burning to restore a mosaic thought to be important for wildlife. For example, in mountain big sagebrush, prescribed burning, even at modest fire rotations (e.g., 55 years in Idaho, Nelle et al. 2000), can adversely impact sage-grouse if the landscape mosaic is not just right (Nelle et al.

2000). A fire mosaic can also increase the ability of cheatgrass to further destroy sagebrush (Knick and Rotenberry 1997).

Burning sagebrush does not assure restoration of a healthy sagebrush ecosystem, and may delay or prevent restoration, since sagebrush itself does not recover for 35 or more years (Figure 1). Restoration of native plants may not require sagebrush thinning (Anderson and Inouye 2001), but if thinning is thought to be needed, fire is inappropriate, as it does not thin sagebrush, but kills it in patches. If fire occurs, successful recovery of the sagebrush ecosystem is enhanced by abundant, healthy native plants (Anderson and Inouye 2001). Restoring native plants is an essential goal before fire is reintroduced or even allowed to continue, if further conversion to cheatgrass is to be avoided (Bunting et al. 2003). Intentional fire suppression is appropriate, at least in Wyoming big sagebrush and the lower elevations of mountain big sagebrush where replacement by cheatgrass is possible (Wambolt et al. 2002). Restoration requires enough solution to the cheatgrass problem to allow some re-seeding or passive re-invasion and increase of native plants, followed by decades of rest or reduced livestock grazing, some fortuitous wet periods, and considerable patience (Anderson and Inouye 2001). Sagebrush ecosystems did not historically burn often or recover quickly, but can be destroyed quickly if we fail to stop the cheatgrass-fire cycle and if we do not focus on restoring the native plants that are essential to maintaining a sagebrush ecosystem that can recover after fire.

Acknowledgments

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Review

Fire and restoration of piñon–juniper woodlands in the western United States: a review

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Abstract

Piñons and junipers, that dominate many semi-arid landscapes in the western United States, have invaded some sagebrush and grassland areas and possibly increased in density since EuroAmerican settlement. Exclusion of fire by livestock grazing and intentional suppression is thought to have been a cause of these changes. National assessments suggest that many woodlands have missed one or more low-severity surface fires and are thus in poor condition, requiring restoration. We undertook a systematic review of seven questions about fire history, fire severity, and the role of fire in these woodlands to evaluate the scientific basis for the national assessment. First, unless piñons and junipers record fire by means of fire scars, it will be difficult to reconstruct fire history. Evidence suggests that most species of piñons and junipers can record fire by means of scars, but scars may be uncommon or absent in some cases and common in others. This variability in scarring has competing explanations that are poorly substantiated. Second, evidence exists for at least three modes of low-severity surface fires in these woodlands: (1) spreading surface fires, (2) patchy surface fires of small extent, and (3) an absence or near absence of surface fires. Methodological problems limit our ability to assess how common each mode is, but spreading, low-severity surface fires were likely not common. Third, there are no reliable estimates of mean fire intervals for low-severity surface fires in these woodlands because of methodological problems. Fourth, fires can kill small trees in true savannas and grasslands, helping to maintain a low tree density, but in most piñon–juniper woodlands low-severity surface fires do not consistently lower tree density and may become high-severity fires. Fifth, nearly all observed fires since EuroAmerican settlement in these woodlands were high-severity fires. In only two studies is there sufficient information to allow a conclusion about whether high-severity fires have or have not increased since settlement, and in these cases the authors conclude they have not. Sixth, the fire rotation for high-severity fires is estimated in only two studies, 400 years in one case, 480 years in the other. Finally, fires may in some cases burn with mixed severity. In conclusion, national fire plans and assessments of the condition and health of piñon–juniper woodlands in the western United States are based on premature and likely incorrect conclusions about the natural fire regime in piñon–juniper woodlands. Local research is essential, at the present time, if effective, scientifically based restoration prescriptions are to be derived.

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Keywords: Piñon–juniper; Woodland; Fire history; Restoration; Ecosystem health; Western US

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1. Introduction

“The shaggy bark of the juniper made fire brands to Satan’s liking. Flaming strips of this bark, often 2 feet or more in length, were hurled ahead to wrap themselves around other trees which caught fire with a roar and gave off ropelike strips of bark to repeat the process” (Hester, 1952, p. 27, describing a 1950 high-severity fire in piñon–juniper)

Woodland conifers in the genera *Pinus* (piñons) and *Juniperus* (junipers) dominate millions of hectares in the western United States (Mitchell and Roberts, 1999). Trees in piñon–juniper woodlands are, in places, increasing in density and expanding into adjoining sagebrush shrublands and grasslands, which is often considered degradation. Causes are thought to be fire exclusion, livestock grazing, climatic fluctuations, and other factors (West and Young, 2000). Yet, it is difficult to determine which factor is most important or how each factor has contributed to change. Fire, the subject of this review, is thought by some to have been frequent enough, before exclusion, to have maintained low-density piñon–juniper savannas and woodlands in some areas and to have prevented tree invasion into sagebrush and grasslands (Gottfried et al., 1995; West, 1999; Brown et al., 2001). However, in other areas, evidence of low-severity surface fire is lacking, and the natural fire regime was dominated by high-severity fires (Floyd et al., 2000). Low-severity surface fires are those that burn primarily in surface fuels, leaving a high percentage of overstory trees alive. High-severity surface fires that kill most overstory trees and high-severity crown fires are lumped here as “high-severity fires” as they cannot be separated in the pre-EuroAmerican record. A “mixed-severity fire” is one that burns partly as a low-severity surface fire and partly as a high-severity fire.

There is interest in restoring piñon–juniper woodlands, sagebrush, and grasslands, that are considered degraded, often by simply removing or reducing piñons and junipers (e.g., Brockway et al., 2002). This is controversial because most past tree removals aimed to increase forage for livestock, but often failed to provide lasting benefit and had adverse effects on wildlife (Lanner, 1977; Despain, 1987). Thinning also may be inappropriate where the fire regime lacked low-severity surface fires (Romme et al., 2003). Yet, new proposals for tree removal have been made or are

being considered (e.g., Pieper et al., 2002), including thinning trees (Bledsoe and Fowler, 1992; Jacobs and Gatewood, 1999; Brockway et al., 2002). Proposals for restoration of piñon–juniper ecosystems often omit a consideration of the role of fire (e.g., Brockway et al., 2002), perhaps because fire in these woodlands is poorly understood (Gottfried et al., 1995; Paysen et al., 2000; Miller and Tausch, 2001). In addition, national-level policy for fire management and woodland restoration is being guided by coarse-level classification of piñon–juniper fire regimes, yet these fire-regime classifications do not agree (Frost, 1998; Brown, 2000; Hardy et al., 2000). It was unclear to us at the outset whether the disagreement is a matter of interpretation or of fundamental uncertainty in the state of present knowledge.

We undertook a systematic review to address these and other unresolved questions about fire history and fire effects on trees relevant to restoration of piñon–juniper woodlands and savannas in the 11 western states (Fig. 1). In a systematic review, before gathering and analyzing studies, criteria are specified for: (1) searching for studies, (2) including a study, (3) assessing the quality of evidence, (4) extracting evidence, and (5) comparing evidence (Englund et al., 1999; Gates, 2002). Systematic reviews have become essential in scientific fields, such as medical research, where economic or health stakes are high and studies offer inconsistent or contradictory results (Egger et al., 2001). Many conservation or restoration questions also have high stakes and may benefit from systematic review (e.g., Bender et al., 1998; Hartley and Hunter, 1998). A systematic review may become a statistically rigorous “meta-analysis” if data can be analyzed as “effect sizes” (Gates, 2002), but this is not possible with the questions we address. However, non-statistical systematic approaches can still improve narrative reviews by reducing reviewer bias.

2. Methods

We identified questions about fire history, fire severity, and fire effects on trees in piñon–juniper woodlands (Table 1). Questions 1–3 ask primarily about low-severity surface fires. Question 4 asks about the effects of fires on tree populations. Questions 5–7 ask about mixed- and high-severity fires.

woodlands, we simply suggest the possibility of this type of fire, which has been documented in other ecosystems.

3.8. Conclusions

Fire history and the effects of fire in piñon–juniper woodlands remain poorly known and understood, as suggested by previous reviewers and authors (Gottfried et al., 1995; West, 1999; Miller and Tausch, 2001). We have more explicitly identified areas of disagreement and uncertainty. For low-severity surface fires, there is substantial uncertainty about the reliability and representativeness of the available fire-scar evidence. Limited success in cross-dating fire scars on piñons and junipers means that most of the piñon–juniper zone in the West lacks reliable evidence of the occurrence and frequency of low-severity surface fires.

There is some reliable evidence that low-severity surface fires may have occurred in the upper ecotone. Yet, while low-severity surface fire regimes remain plausible for other areas, there are almost no direct fire data supporting the notion of frequent low-severity surface fires maintaining savannas or most woodlands. No reliable data suggest that low-severity surface fires occurred or would have consistently lowered the density of trees in moderate-density woodlands with a sagebrush or grassy understory. The closed woodland zone in much of the West, moreover, has virtually no evidence for spreading low-severity surface fires.

In fact, at least on a regional basis, some woodlands did not experience low-severity surface fires, but, rather, were naturally subject to long-rotation high-severity fires. Thus, arguments that piñon–juniper woodlands have become more dense due to fire suppression in these areas seem unlikely. Consequently, fire suppression is not clearly a cause of modern high-severity fires; in some places these high-severity fires are natural, and in much of the rest of the West their occurrence prior to EuroAmerican settlement is unknown. Fires, that are effectively high-severity fires, since they may kill stands consisting primarily of small trees, are well-documented in one case to have been able to prevent tree invasion into sagebrush and grasslands prior to EuroAmerican settlement. However, absence of these fires in another pre-EuroAmerican case did not lead to tree invasion. Thus, the role of fire as a general mechanism maintaining the ecotone

and the role of fire suppression in encouraging tree invasions remain poorly supported and uncertain. Variability in the abundance of fire scars and in reports of pre-EuroAmerican high-severity fires and low-severity surface fires suggest that regional and even possibly within-site variation in fire regimes could be substantial. But more specific knowledge of fire regimes is lacking or uncertain for most of the piñon–juniper woodland area in the West.

In spite of these uncertainties, the fire regime of piñon–juniper woodlands has been classified by researchers and used by land managers to assess woodland condition and ecosystem health. These classifications and assessments are not supported by the scientific literature we reviewed. In creating maps of fire regimes, Frost (1998) uses Leopold (1924), apparently as the sole source, to place piñon–juniper woodlands into a “13–25 years” fire-frequency class, even though our review suggests there are many other sources that do not support this classification. Brown (2000) maps piñon–juniper as “Mixed-severity fires 0–34 years.” Our review shows that reliable evidence of individual fires of mixed severity is lacking, and fires of higher severity are likely much less frequent than 0–34 years (Section 3.6).

Hardy et al. (2000) is the basis for rating piñon–juniper woodland condition across the West relative to the effects of fire suppression. Hardy et al., based on the expertise of local fire managers, classify the piñon–juniper fire regime as “0–35 yr frequency, low severity,” a classification not supported by the scientific evidence we review here. Since these authors place piñon–juniper woodlands mostly within a low-severity, frequent-fire class, these woodlands are considered to have missed two or three fires in the last century. However, our review suggests that, while uncertain, low-severity surface fire was most likely not a common type of fire in piñon–juniper woodlands in the western United States. In some parts of the West, the natural fire regime of piñon–juniper woodlands was clearly dominated by high-severity fires. The condition assessment or Hardy et al. (2000) is thus definitely erroneous for these areas of woodland, likely is in error for much of the rest of the West, and is at best premature given the uncertainty our review identifies. At the present time, our review suggests there is insufficient scientific basis for a national program that rates woodland condition and then applies uniform fire and structural

restoration treatments in piñon–juniper woodlands across the West.

If restoration of fire in piñon–juniper woodlands is to be based on sound science, significant methodological hurdles (i.e., modern calibration, cross-dating) must first be addressed and resolved. Only then can fire scientists focus on systematic collection and analysis of the key evidence that can distinguish and quantify the types of fires that occurred in the past. If a network of such studies were available, then a science-based national restoration program could probably be effectively created.

Until this is possible, we suggest a more cautious, research-based local restoration strategy. Localized or site-specific scientific studies are always needed before restoration prescriptions are formulated (Romme et al., 2003), but this is particularly true now, given the uncertain state of the science. We suggest that before undertaking restoration treatments on a particular site, managers or scientists date some of the largest trees on the site. If these trees pre-date EuroAmerican settlement, removing or thinning them is inappropriate if restoration is the goal. Trees that pre-date EuroAmerican settlement represent woodland structure before the impacts of our land uses, and thus need to be preserved during restoration as is true in other ecosystems (e.g., Friederici, 2003). Moreover, old-growth piñon–juniper woodlands have many ecological values that have been under-appreciated (Waichler et al., 2001).

If larger trees on a site post-date EuroAmerican settlement, the stand could represent either (1) piñon–juniper invasion into vegetation that was not previously woodland or (2) natural re-establishment of piñon–juniper following a fire in a former woodland. Natural re-establishment of trees after fire can be quite slow in these woodlands, requiring decades, so that post-fire stands may superficially appear to represent tree invasion. However, post-fire stands can often be identified by the presence of some standing or down charred wood from the fire. Burned woodlands with slowly re-establishing trees do not warrant treatment if the goal is restoration. Invading post-settlement stands and post-settlement trees inside old stands require further research to determine whether restoration is needed, and, if so, what needs to be done. Invasion may be natural (e.g., climatic fluctuations) or human-caused (fire suppression, livestock grazing,

increased carbon dioxide). Unless the specific natural or human causes can be distinguished for a site, restoration is likely to be ineffective or possibly mis-directed. The first step in effective restoration is to identify and then modify the cause of degradation (Hobbs and Norton, 1996). If our land uses are found to be responsible for tree invasions or density increases, and if restoration is to have lasting value, it is essential to change the land uses that led to the need for restoration.

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AVIAN COMMUNITIES IN THE PINYON-JUNIPER WOODLAND:

A DESCRIPTIVE ANALYSIS

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ABSTRACT

The expansive range and elevational distribution of the pinyon-juniper woodland in the western United States contributes to the wide variety of forms of this habitat type. Similarly, the breeding-bird community expresses this variety. A total of at least 73 different bird species are known to breed here. About 31 of these species breed with regularity in pinyon-juniper woodlands. Only about 5 of these species are restricted to this habitat type. Usually less than half of the breeders are permanent residents. A high proportion of the breeding birds forage for seeds or insects on the ground. The number of species that breed in cavities and/or forage on trunks and branches is positively correlated with pinyon pine density. Seasonal densities of breeding birds vary greatly depending on annual fluctuations in precipitation and seed and berry production. Winter diversity and density is strongly correlated with juniper berry production. Both junipers and pinyons show an adaptive suite of characters for dispersal by birds.

KEYWORDS: pinyon pine, juniper, avifauna, guilds, diversity, density, breeding-birds, winter birds.

The pinyon-juniper woodland could be labeled the characteristic habitat-type of the southwest because of its expansive range.

Extending over large areas of Arizona, Colorado, Nevada, New Mexico, and Utah it occupies somewhere between 43 and 76 million acres of land in the West. In New Mexico alone the woodland covers over 32,000 square miles or 26 percent of the state (Pieper 1977). The woodland stretches from the east slope of the Sierras to Oklahoma and from Oregon to Texas and into Mexico. It is the common vegetation-type of the foothills, low mountains, escarpments, and mesas of the southwest (Fig. 1). Throughout its range this "pygmy forest" shows broad tolerance limits ranging in elevation from a high of 10,000 ft. in the Sierras to a low of 3200 ft. in the four corners area, with junipers alone extending even lower in many areas (West et al. 1975). It is found on a variety of soils derived from granite, basalt, limestone, and mixed alluvium (Hurst 1975).

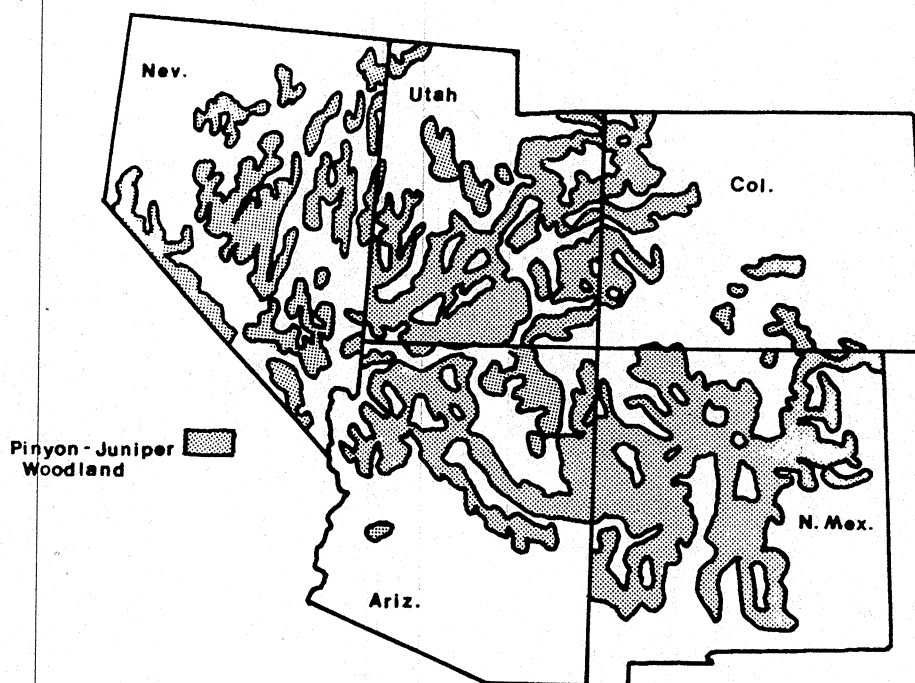


Figure 1. The distribution of pinyon-juniper woodland in the five western states where it is most abundant (From Clary 1975).

The major trees of this woodland consist of four species of junipers, Juniperus occidentalis, J. deppeana, J. monosperma and J. osteosperma. The latter species is the most wide-spread of the junipers. The two most common pinyon pines are Pinus monophylla and P. edulis with the latter species having the most extensive distribution. The dominant trees of the area are relatively small (hence the name pygmy forest) ranging in height from 15-40 ft. with individual trees having dense foliage. In general the junipers are more drought-resistant than pinyon pines and therefore occur in highest densities at lower elevations, whereas, pinyon pines become more abundant at higher elevations in this woodland (Short and

McCullock 1977). The density of these trees varies from very sparse to very dense depending on elevation, climate, and soil type. Total plant cover increases with elevation up to about 6600 ft. (Tueller et al. 1979).

The understory vegetation of the pinyon-juniper woodland is highly variable depending on soil type, exposure, and climatic pattern. Tueller et al. (1979) lists 240 positively identified species of vascular plants from the Great Basin pinyon-juniper woodlands. The list includes 67 species of shrubs and succulents, 46 grasses, and 122 forbs that grow under pinyon and juniper trees. Major shrubs include sagebrush (*Artemisia* sp.), bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* sp.), and various species of oaks (*Quercus* spp.). Few of these species are found growing in association with one another, as the understory is reasonably depaupered. None of the shrubs, succulents, grasses or forbs are listed as rare and endangered and none are restricted to this vegetation type. Most woodlands contain only a few of these species. Thus, plant species diversity (as well as density) is reasonably low compared to other vegetation types in the southwest.

The climate of this vegetation-type can be summarized as being rather severe with hot summers, cold winters, low amounts of precipitation in the form of rain and snow, low relative humidity and high winds. Mean daily maximum temperatures for the hottest month of the year vary from 26°C to 36°C. Total yearly precipitation varies between 8 and 18 inches (West et al. 1975).

The lower limits of this woodland now mingle with grassland, desert scrub, Great Basin Desert or shrublands in different parts of its range. Because of climatic cycles (cool, moist to hot, dry) this lower boundary has been very active during the last 10,000 years (Martin and Mehringer 1964, Wright et al. 1973, Wells and Berger 1967). Evidence from pollen deposits, sloth dung, and wood rat middens indicate a considerable lowering of this boundary. This depression caused isolated areas of the woodland to come into contact with other such areas thus increasing the potential for redistribution of the flora and fauna. The return of a warmer, drier climate caused an upward retreat leaving behind isolated relict pockets of pinyon-juniper woodland, with its faunal components.

Even though early settlers heavily used pinyons and junipers for mine props, fence posts, and fuel, during the last 130 years the vegetation type is undergoing an expansion into low shrublands, grasslands and Great Basin Deserts (West et al. 1975). At the same time the density of trees in more permanent stands is also increasing. Numerous causes have been proposed to explain this increase, but the major culprit seems to be overgrazing by cattle and sheep (Aro 1971). Improper grazing has reduced forage production thereby releasing the trees from competition with the herbs and shrubs. Johnsen (1962) believes the spread of juniper in northern Arizona is due to the increased spread of seeds by livestock, lack of periodic fire, overgrazing which reduces competition of grasses with juniper seedlings, and a gradually changing climate which favors the spread of juniper. La Marche (1974) presents evidence that the period from 1850 to 1940 was wetter and warmer than the period before or after this.

It is evident that this woodland as a whole is an extremely complex, variable community. As stated by West et al. (1975), "Early attempts to explain distribution, composition, successional changes, and management responses in terms of single factors were overly simplistic. These variations can be better explained in terms of a complex of environmental patterns, historical events, and successional mechanisms. The relative importance of each factor of the environmental complex varies with the synecological context."

A major characteristic of this woodland as far as birds are concerned is the periodic production of vast quantities of pinyon pine seeds and juniper berries. Large crops of pine seeds are produced once every five or six years whereas juniper berry production occurs every two to three years. In many years neither tree forms reproductive propagules. Both life-forms appear to have intra-specific synchrony. For example, in a year of a good berry crop, one hectare contains between 19 and 38 million berries. A cubic meter of foliage holds 20,000 berries. The number declines steadily through the late fall and winter as birds and mammals consume them. The flesh of a single berry has about 315 calories making it a desirable source of energy. The berries are a shiny blue in color making them conspicuous; they ripen in the fall when insects are sparse and bird densities are high due to migration (Salomonson 1978). Thus junipers have adaptations favoring zoochory (Morton 1973). The pinyon pine also has a constellation of adaptations that favor dispersal by animals, especially birds (Table 1) (Vander Wall and Balda 1977). This pine not only allows animals easy access to its seeds but may entice dispersal agents. This means the seeds are easily located, extracted from the cones and eaten or cached for future use (Vander Wall and Balda 1977, Ligon 1978). More *Pinus edulis* seeds are cached in dry, exposed soils than can be used by the birds in years of high cone crops. In some years, pinyon pines produce absolutely no cones per hectare (Balda, unpubl. data), whereas in other years they may produce as many as 1800 cones/tree (Ligon 1971). These seeds are extremely nutritious, containing about 7400 cal/g (Little 1938). A pinyon pine seed contains 14.5 percent protein, 60 percent fat, and 18.7 percent carbohydrate (Botkin and Shires 1948). The large size, high energy content, and high protein level makes this seed a highly desirable food stuff.

Management of pinyon-juniper woodlands since the mid-40's has largely consisted of control of the spread of junipers (and in some cases pinyon) into grasslands and type-conversion of pinyon-juniper woodlands into grazing lands. Both eradication of the type and control has been justified on public lands because the trees are generally considered as of low commercial value relative to other harvestable trees of the West. During the period 1950 to 1964 Box et al. (1966) estimate that approximately three million acres of pinyon-juniper woodland were converted to grazing lands. Between 1950 and 1961, more than one million acres were converted in Arizona alone (Arnold et al. 1964).

The major objective of most type-conversion projects, often referred to as "Range Improvement Projects" is to produce additional forage for livestock (Terrel and Spillett 1975). These conversions represent "a change from multiple use to one use, grazing" (Little 1977). Land managers today are going through a period of cautious

2-3 yrs
juniper

soul-searching about how to proceed with management on these lands. This treatment has not been popular, leaves the area an aesthetic diaster, has questionably proven long range benefits and "Most questions concerning wildlife and pinyon-juniper range conversion are unanswered and probably will remain so." (Terrel and Spillett 1975). The best synopsis of pinyon-juniper management and guidelines for future use can be found in a symposium edited by Gifford and Busby (1975).

TABLE 1. Features of pines with different dispersal strategies

Characteristic	<u>P. ponderosa</u> (wind)	<u>P. edulis</u> (animal)
Seed size	small	large
Seed conspicuous	no	yes
Seed quickly released	yes	no
Seed coat labelled	no	yes
Synchronous cone opening	yes	no
Position of cone	down, out	up, out
Cone scales	present	absent

BREEDING BIRDS

A total of 73 different species of birds are reported to breed in pinyon-juniper woodlands (Table 2). Undoubtedly more records are known but these will most often be rare or unusual occurrences. These 73 species are taxonomically aligned in 8 orders and 25 families. Because of the geographic area span by this plant community and the wide physiognomic variety (over its range) no one area contains near this breeding diversity. For example, in north-central Arizona 5 pinyon-juniper plots were sampled intensively during two breeding seasons (Grue 1977, Masters 1979) and the number of breeding species per 40 ha plot ranged from 12 to 24 and averaged 19 species. Rasmussen (1941) reports 43 species inhabiting the pinyon-juniper woodland on the Kaibab Plateau in summer but has good evidence for breeding by only 12 species. Hardy (1945) lists 22 species as regular breeders in Utah pinyon-juniper woodlands whereas Hering (1957) reports 15 breeding species.

Relatively few of the 73 species are restricted to pinyon-juniper woodland. Table 2 lists 5 obligates and 13 semi-obligates. An obligatory species is defined for purposes of this presentation as one which nests only in pinyon-juniper woodland within a geographic area that contains other habitat types. A semi-obligatory species may nest in one additional plant community. This definition is knowingly broad as most of these species nest in different habitat types in portions of their range where pinyon-juniper woodland is absent. Hardy (1945) mentions only the Piñon Jay and Plain Titmouse as being obligatory and the Bushtit as a semi-obligatory species in this woodland type. But, the Piñon Jay often nests and forages in ponderosa pine forest (Balda and Bateman 1971) and the Bushtit is also known to use other habitats.

I/ Scientific names for all birds mentioned in the text or tables are given in Appendix I.

TABLE 2. Breeding birds of pinyon-juniper woodlands¹⁾

Species	Status ²⁾	Distribution ³⁾	Niche Width ⁴⁾
Turkey Vulture ✓	S	4	
Cooper's Hawk ✓	p	2	
Red-tailed Hawk ✓	p	4	
Swainson's Hawk ✓	S	1	
Ferruginous Hawk ✓	p	2	
Golden Eagle ✓	p	3 (Sp.)	
Prairie Falcon ✓	p	2 (Sp.)	
American Kestrel ✓	p-S	4	
Gambel's Quail	p	2	
Mourning Dove ✓	p-S	7	
Screech Owl ✓	p	3	obligatory
Great Horned Owl ✓	p	3	
Long-eared Owl ✓	S	1	
Saw-whet Owl ✓	p	1	
Poor-will ✓	S	2	
Common Nighthawk ✓	S	3	
Lesser Nighthawk	S	2	
White-throated Swift ✓	S	2 (Sp.)	
Black-chinned Hummingbird	S	4	semi-obligatory
Costa's Hummingbird	S	1	
Broad-tailed Hummingbird	S	3	
Common (red-shafted) Flicker ✓	p	6	
Hairy Woodpecker ✓	p	4	
Ladder-backed Woodpecker	p	1	
Western Kingbird	S	1	
Cassin's Kingbird	S	2	
Ash-throated Flycatcher	S	7	semi-obligatory
Say's Phoebe	S	2	
Gray Flycatcher	S	2	obligatory
Western Wood Pewee ✓	S	1	
Violet-green Swallow ✓	S	2	
Cliff Swallow ✓	S	1 (Sp.)	
Scrub Jay	p	6	obligatory
Black-billed Magpie ✓	p	2	
Common Raven ✓	p	6	
Piñon Jay ✓	p	5	semi-obligatory
Mountain Chickadee ✓	p	3	
Plain Titmouse	p	7	obligatory
Bushtit	p	6	semi-obligatory
White-breasted Nuthatch ✓	p	3	
House Wren ✓	S	1	
Bewick's Wren	p-S	3	semi-obligatory
Cañon Wren ✓	p-S	3 (Sp.)	
Rock Wren ✓	p-S	4	
Mockingbird	S	4	semi-obligatory
American Robin ✓	p-S	1	
Western Bluebird ✓	p-S	1	
Mountain Bluebird ✓	p-S	4	
Blue-gray Gnatcatcher	S	5	semi-obligatory
Loggerhead Shrike ✓	S	2	

36 +
12
51

TABLE 2. (cont.)

<u>Species</u>	<u>Status</u> ²⁾	<u>Distribution</u> ³⁾	<u>Niche Width</u> ⁴⁾
Gray Vireo	S	3	obligatory
Solitary Vireo ✓	S	2	
Black-throated Gray Warbler	S	5	semi-obligatory
Scott's Oriole	S	3	
Brown-headed Cowbird ✓	S	4	
Hepatic Tanager	S	1	
Black-headed Grosbeak ✓	S	5	
Lazuli Bunting ✓	S	2	
Cassin's Finch ✓	S	1	
House Finch ✓	P-S	5	semi-obligatory
Lesser Goldfinch	S	2	
Red Crossbill ✓	S	1	
Green-tailed Towhee ✓	S	2	
Rufous-sided Towhee ✓	P	6	semi-obligatory
Brown Towhee	P	2	semi-obligatory
Vesper Sparrow ✓	P-S	2	
Lark Sparrow ✓	S	4	semi-obligatory
Black-throated Sparrow	P-S	3	
Sage Sparrow	S	1	
Dark-eyed Junco ✓	S	1	
Gray-headed Junco	P-S	1	
Chipping Sparrow ✓	P-S	6	
Brewer's Sparrow ✓	S	1	
Black-chinned Sparrow	P	2	semi-obligatory
Total: n = 74	P = 23 (32%) S = 38 (51%) P-S = 13 (17%)	s-o = 13 o = 5	

- 1) Data from Rasmussen (1941), Hardy (1945), Miller (1946), Hering (1957), Grue (1977), Masters (1979)
- 2) P = permanent resident; S = summer resident
- 3) The number indicates the number of census plots or study areas used for breeding. The maximum is 7. Sp. = special landscape required.
- 4) Obligatory = in a given geographic area the species breeds only in the pinyon-juniper woodland; semi-obligatory = same as above but breeds in one additional plant community.

Few, if any other natural habitat-types in North America have so few truly obligatory species. The reason(s) such should be the case is not clear but may relate to the great physiognomic diversity found in the pinyon-juniper woodland. Just as there is no typical pinyon-juniper woodland there are few obligate pinyon-juniper birds.

Just as the number of breeding species varies between woodlands so does breeding bird density. In southwestern Arizona where many oaks are found in the woodlands breeding bird density may reach 250 pairs per 40 ha (Balda 1967). This density is seldom if ever reached in the pinyon-juniper woodland where densities vary between 30 and 190 pairs

per 40 ha (Table 3). Ninety-five pairs is about an average figure. Grasslands usually have fewer breeding pairs and ponderosa pine forests more than the pinyon-juniper woodland.

TABLE 3. Characteristics of the avian woodland breeding birds

Study	Habitat	No. of Breeding Species	No. of Breeding Pairs/40 ha
Balda, 1967	oak-juniper	36	224
Balda, 1967	oak-juniper-pine	36	267
Grue, 1977	juniper-parkland	17-23	54-179
Beatty, 1978	juniper-grassland	11-12	35-40
Grue, 1977	juniper-pinyon	24-26	66-130
Masters, 1979	pinyon-juniper I	9-10	90-87
Masters, 1979	pinyon-juniper II	18-21	191-138
Masters, 1979	pinyon-juniper III	19-19	122-133
Hering, 1957	pinyon-juniper (?)	15	33
Beidleman, 1960	pinyon-juniper	2	30
Hardy, 1945	pinyon-juniper	22	--
Miller, 1946	pinyon dominated	55	--

Breeding bird densities in a single location show rather large annual fluctuations that appear to be linked to biotic and physical factors. In very dry years the breeding bird populations may be reduced between 50 and 70% (Grue 1977). Possibly pinyon pine seed crops may attract breeding birds the next spring. Masters (1979) found a 28% increase in populations after a large cone crop (Table 4).

Table 4. Changes in breeding bird densities (pairs/40 ha) and diversities between years

Study	First Year Density/Diversity	Second Year Density/Diversity	%Change	Reason
Masters, 1979	191/21	138/18	28/14	Pinon seed crop before first year
Grue, 1977	130/26	66/24	49/8	Annual fluctuation in precipitation
Grue, 1977	179/23	54/17	70/26	Same as above

Masters (1979) attempted to explain the relationship between various habitat parameters and characteristics of the breeding bird

fauna. At the level of the community, she found that the number of breeding bird species was significantly correlated with a) the density of pinyon pine, b) total tree density and c) pinyon pine foliage volume. Foliage height diversity (as measured in two-meter height classes) was a significant predictor of bird species diversity. Breeding bird density was significantly correlated with pinyon pine density when the bird population figures following a large pinyon pine cone crop are ignored.

A "typical avifauna" of the pinyon-juniper woodland thus appears to be as simplistic an approach as trying to describe a typical vegetation for this woodland type. Never-the-less we have selected from the list of 74 breeding species a group that has a distribution score (Table 2) of four or higher and/or is listed as obligatory or semi-obligatory in niche width. A major danger here is that two closely related species may be sympatric and thus neither would have achieved the criteria for inclusion. Such could have been the case for nighthawks, kingbirds, hummingbirds, bluebirds, medium-billed sparrows and a few other cases. In these instances the most common of the dyad or triad was added to the list to make it as representative as possible. From Table 2, 29 species met the first criteria and the nighthawk and kingbird were added for reasons given above.

Resident Status

Of the 31 species that fit our "typical avifauna" criteria 14 (45%) are summer residents and 11 (35%) are permanent residents. Six species show variable patterns of residency either based on geographic considerations (i.e. summer residents in the northern portion of their range and permanent residents in the more southern areas) or variable weather conditions (i.e. migrate in harsh winter, remain stationary in mild winters). Hardy (1945) in eastern Utah described 36% of the nesting species as permanent residents and 64% as summer residents, almost identical to our typical avifauna if one includes the "switchers" in the summer category.

Data from intensively censused plots in central Arizona over a two year period showed about the same split as does the Utah data (Grue 1977). The proportion of permanent resident species ranged from 35 to 40%.

In north-central Arizona however, Masters (1979) censusing three pinyon-juniper plots for two years found a range of permanent resident breeders from 32 to 56% (Table 5), and Hering (1957) near Mesa Verde, Colorado had 53% permanent residents. One could expect permanent residency to increase in the woodlands with decreasing latitudes but such an increase is not apparent from either the proportion of the breeding population that is permanent or the absolute number of species that do so. On both of Masters' (1979) plots with proportion of permanent residence above 50% the ratio of pinyon to juniper trees was better than 2:1. (Hardy's 1945 ratio was 0.36 to 1). Hering (1957) did not provide the necessary data to assess this habitat feature but the general area of her study contains high densities of *P. edulis* (pers. obs. R. P. Balda). Of the 55 species of breeding birds (a woodland high) listed by Miller (1946) in a southern California woodland predominated by pinyon pine, 27 species or 49% were apparently permanent residents. Two areas without pinyons had 33 and 35%

permanent resident breeders. Thus, we suggest with caution that a positive correlation may exist between the proportion of permanent residents in the community and the proportion of trees in the woodland that are pinyon pines. In all probability no one factor will answer the question, but this one does deserve future investigation. Of the 18 species listed as either obligatory or semi-obligatory in this woodland 8 are permanent residents.

Table 5. Residence status of breeding birds from specific sites in north-central Arizona (Masters 1979)

Status	Number of Species (%)		
	I	II	III
Permanent Resident	3.0* (32)	8.0 (53)	7.5 (56)
Summer Resident	6.5 (68)	7.0 (47)	6.0 (44)

* 2 yr. average

Foraging Guilds

An instructive way to look at avian communities is the use of foraging guilds (Root 1967). A guild is defined as one or more species in a community that use similar foraging techniques. Guilds can be defined as broadly or narrowly as the observations and data base permit. Here for the sake of simplicity and accuracy (but sacrificing specifics) I define foraging guilds only by substrate-type. This is done because very little information is known about the species under consideration to allow for finer distinctions. Foraging guilds used include ground, foliage, air, bark, and flowers. If a species used two of these substrates I assigned half the value to each guild.

The descriptive analysis from nine different intensively studied woodland sites shows few trends. The number of ground foragers varied from 6 (Hering 1957) to 16 (Grue 1977) species. Relative proportions of ground foragers varied between 40% (Hering 1957) and 57% (Grue 1977). No significant correlation (Spearman Rank Correlation) between the density of pinyon pine or juniper and either the number or proportion of ground foraging species was found.

The number of foliage foragers in the breeding community varied from a low of three in a juniper-grassland (Beatty 1978) to a high of 12 in a predominantly pinyon pine stand. The mean number of species that used foliage as a substrate where both pinyon and junipers were represented was 5. The number or proportion of foliage foraging species showed no significant correlation with pinyon or juniper density.

The number of species of hummingbirds (nectar feeders) also shows no correlation with tree species density. Hummingbirds most likely respond more to the species composition and flowering patterns of the shrub and forb strata which may be limited by physical factors (temperature, moisture, etc.).

There is also no trend for aerial feeders. Aerial foraging species number between 1 (Hering 1957) and 9 (Miller 1946). On areas containing both pinyon and junipers the mean number of aerial feeders was 4.

In some woodlands a small group of breeding species forage extensively on trunks and large branches. In no intensive study area analyzed for this report where the ratio of pinyon to junipers was less than 1:1 did any of these species breed. Where pinyons outnumbered junipers by 2:1 or better two species appeared. Almost invariably these two species were the Hairy Woodpecker and White-breasted Nuthatch. The former species obtains insects by hammering holes through the bark or flaking layers of bark off in small plates. The latter species probes the crevices in the bark to obtain insects. Both species reach higher densities in ponderosa pine forests (Szaro and Balda 1979) than in the woodlands. Either there are more insects in, under, and on pinyon pine bark than juniper or the bark pattern is such that insects are easily extracted.

The "typical avifauna" for pinyon-juniper woodlands has a slightly higher number of ground and foliage foragers than the studies described above (Table 6). This probably occurred because our selected sample of birds is slightly larger than would be found in any one woodland area.

Table 6. Foraging Guilds for a "typical pinyon-juniper woodland"

Guild	* Number of Breeding Species (%)
Ground	14.5 (52)
Foliage	7.0 (24)
Aerial	4.5 (16)
Bark	1.0 (4)
Flower	1.0 (4)
*Carnivores not included	

The above analysis has dealt solely with numbers of species because of the high year-to-year variability in densities. Master's (1979) regression models to predict characteristics of the bird populations included foraging guilds. Eight independent foliage variables were used. Pinyon density was significantly correlated with densities of aerial feeders, bark feeders, and total density of all insectivorous birds (Table 7). No variable contributed solely by junipers was important as a predictor of any of the breeding bird characteristics measured. Why the above result should occur is not immediately obvious but suggests pinyon pine may provide a more suitable foraging substrate than juniper.

Only fragmentary data exists to support the contention that juniper is less attractive as a foraging substrate than is pinyon pine. In an oak-juniper-pine (*Pinus cembroides* and *P. leiophylla*) woodland in southeastern Arizona, Balda (1969) studied foliage use by the 36 breeding species. The number of observations in each tree species were compared to the foliage volume contributed by each tree species. Based on foliage volume an expected number of bird observations per tree species was calculated. Actual foraging

observations in juniper were far less than expected, whereas foraging observations in pines were much greater than expected. At that time Balda proposed that the breeding birds may simply have not yet learned to use juniper as it is known that juniper is presently spreading into new areas and increasing in areas where it was once sparse. The Black-throated Gray Warbler, Chipping Sparrow, Bridled Titmouse and Common Bushtit utilized juniper more than any other species. Three of the four species listed above are members of our "typical woodland avifauna." In a pinyon-juniper-ponderosa pine ecotone Laudenslayer and Balda (1976) found that pinyon pine was selected more intensely than predicted by expected numbers generated from foliage volume. Juniper was selected approximately as often as expected. We explained this difference by using the relative proportion of foraging surface within both trees. Although both species have their green foliage concentrated on the outer edges of the branches, needles of pinyon pine are found growing farther inward than in juniper. Thus, if the growing areas and areas of green vegetation on these trees are used as prime foraging surfaces then pinyon provides more of this surface per tree than does juniper.

Table 7. Percent variability explained (r^2) of breeding bird parameters by vegetation factors which are significantly correlated (Masters 1979)

Factor	Density of Feeding Guilds		
	Aerial Feeders	Bark Feeders	Insectivores
Pinyon Pine Density	.980	.781	.949
Total Tree Density	.979	.776	.947
Pinyon Foliage Volume	.902	NS	.834

Insect densities in pinyons and junipers may also be a reason why pinyon density is a good predictor of density of insect eating birds. Masters (1979) found, however, that junipers had a higher number of insect taxa than did pinyon. Insect abundance (as measured by total length) was about the same in both trees. The similarity coefficient (a measure of community similarity) indicated that pinyon and juniper have different arthropod faunas associated with them.

Nesting Guilds

The classification of the avian community by nesting habits may also provide clues as to how breeding birds interact with the structure of the vegetation. Of the 31 species used as a "typical avifauna" 60% (18.5) nested in foliage (the 0.5 is for the Mourning Dove that uses both foliage and ground for a nest substrate), 23% (7) used cavities and the remainder nest on the ground. Hardy's data (1945) fits well with 61% of the breeding birds nesting in the foliage, 21% in cavities, and 18% of the species nesting on the ground.

On two intensively studied plots in central Arizona Grue (1977)

found an average of from 60 to 68% foliage nesting species in the breeding bird community. From 15 to 20% of the species nested in cavities. Again the fit is reasonable with what a "typical avifauna" would show (Table 8).

Table 8. Nesting guilds of breeding birds from specific sites in central Arizona (Grue 1977)

Nesting Guild	Number of Species (%)	
	Pinyon-Juniper Woodland	Juniper Parkland
Foliage	16.5* (66)	14.0 (68)
Cavity	5.0 (20)	3.0 (15)
Ground	3.5 (14)	3.5 (17)
Total	25.0	20.5

* 2 yr. averages

In north-central Arizona Master's (1979) found cavity nesters to make up almost half of the breeding species on areas where pinyons outnumbered junipers (Table 9). Hering (1957) found cavity nesting species made up 47% of the breeding species on an area of presumable high pinyon densities. Both studies had 7 to 8 cavity nesting species present. The pinyon dominated woodland in California (Miller 1946) contained 11 cavity nesting species.

Table 9. Nesting guilds of breeding birds from specific sites in north-central Arizona (Masters 1979)

Nesting Guild	Number of Species (%)		
	I	Sites II	III
Foliage	7.0* (74)	7.5 (50)	6.5 (48)
Cavity	2.0 (21)	7.0 (47)	6.5 (48)
Ground	0.5 (5)	0.5 (3)	0.5 (4)

* 2 yr. averages

The emerging pattern is more than suggestive that cavity nesting species will occur with higher probability in woodlands containing large numbers of pinyon pines. On three study sites in north-central Arizona Masters (1979) found that 79% of the variability (r^2) in density of the combined cavity nesting species (not species numbers as discussed above) was explained by the density of pinyon pines.

Both density and diversity of cavity nesting species may be related to pinyon pine in some manner. Since cavity nesters depend on weakened or diseased trees to excavate cavities in, it is possible that pinyon pine are more prone to attack by insects and other disease

causing organisms. Also, it may be that pinyon branches are more brittle and are therefore more prone to breaking thus allowing disease agents entry. Dead junipers are hard whereas dead pinyon pines contain soft wood (pers. obs.).

The question that remains deals with tree-type selection by the foliage breeding birds: Do foliage breeders select for either juniper or pinyon when choosing a nest site? Both Hardy (1945) and Short and McCulloch (1977) make unsubstantiated comments that foliage nesting birds prefer junipers over pinyons for nest-sites. Based on the amount of data presently available it is not possible to answer that question and more research is required to show if any preference is shown (Table 10). The two species that showed regular use of juniper were the Black-chinned Hummingbird and Black-throated Gray Warbler whereas the Chipping Sparrow showed no preference for either tree (Masters 1979, Balda 1969).

Table 10. Nest sites of foliage nesting birds in western woodlands

Study	Number of Nests in		
	pinyon	juniper	other
Balda, 1967	oak-juniper 67 1	(not present)	1 12
Balda, 1967	juniper-oak-pine 46 46 29	--	11 10
Laudenslayer and Balda, 1976	pinyon-juniper-ponderosa pine 48 46 27	3 --	--
Masters, 1979	pinyon-juniper I 32 33	-- 1	--
Masters, 1979	pinyon-juniper II 87 33	10 5	--
Masters, 1979	pinyon-juniper III 87 34	6 2	--

WINTERING BIRDS

Winter bird populations of the woodland have been studied in central Arizona by Grue (1977) and in north-central Arizona by Shrout (1977). A total of 32 species have been recorded as wintering in these woodlands. These 32 species belong to five orders and 14 families. Of these, 18 are permanent residents, 10 are winter residents, and 4 are switchers. The most regular winter residents are the two species of juncos, White-crowned Sparrow, and Ruby-crowned Kinglet. Three of these four species are seed eaters. Prominent "switcher" species are the Mourning Dove, American Robin, the two bluebirds, and the House Finch. Only the Bushtit, kinglet and wren are insectivorous (Table 11).

Species numbers vary considerably from year-to-year. Shrout (1977) reported a diversity of 10 species in one winter and 20 the next on the same 40 ha plot. Mean number of wintering species in Arizona woodlands is about 15 (Grue 1977, Shrout 1977).

Table 11. Birds wintering in pinyon-juniper woodlands

Species	Status*	Distribution (max = 3)
Rough-legged Hawk	W	1
Merlin	W	1
Prairie Falcon	P	(pers. obs.)
Gambel's Quail	P	1
Mourning Dove	P-S	2
Hairy Woodpecker	P	1
Common (red-shafted) Flicker	P	3
Horned Lark	P	1
Common Raven	P	3
Piñon Jay	P	1
Scrub Jay	P	3
Mountain Chickadee	P	1
Plain Titmouse	P	3
Common Bushtit	P	3
White-breasted Nuthatch	P	(pers. obs.)
Red-breasted Nuthatch	W	(pers. obs.)
Bewick's Wren	P	2
Ruby-crowned Kinglet	W	2
American Robin	P-S	1
Townsend's Solitaire	W	1
Western Bluebird	P-S	1
Mountain Bluebird	P-S	1
Sage Thrasher	W	1
Evening Grosbeak	W	1
House Finch	P-S	2
Cassin's Finch	W	(pers. obs.)
Rufous-sided Towhee	P	1
Vesper Sparrow	P	1
Dark-eyed Junco	W	3
Gray-headed Junco	W	3
Chipping Sparrow	P	3
White-crowned Sparrow	W	3
n = 32	P=16, W=11 and P-S=5	

Winter densities vary greatly from place-to-place and from year-to-year. For example during the winter of 1973-74 Grue (1977) reported 318 individuals per 40 ha in a pinyon-juniper woodland and 251 wintering birds in a 40 ha juniper parkland. This is a 21% difference.

Year-to-year variations are even more striking. In some years the woodland supports huge flocks (too large to count) of bluebirds, American Robins and mixed flocks of juncos. In other years one can walk for hours seeing only a very few birds (Vaughan pers. comm., R. P. Balda pers. obs.). Shrout (1977) found 293 wintering birds per 40 ha in the winter of 1973-74 and 75 individuals during the winter of 1974-75 on the same plot. Using a conservative calculation this is a 74% change in population density between years.



Research Article

Multiscale Models of Habitat Use by Mule Deer in Winter

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ABSTRACT Mule deer (*Odocoileus hemionus hemionus*) populations have experienced widespread declines in much of western North America and alteration or loss of habitat could be contributing to these declines. Consequently, understanding habitat features that are important to mule deer is necessary for effective management of the species and their habitat. From 2005–2012 we radio-marked 452 mule deer with global positioning system collars across 9 distinct winter ranges to evaluate winter habitat use along the east slope of the Cascade Range in south-central Oregon, USA. Using data from 357 mule deer across 9 analysis areas, we developed regional habitat use models for mule deer on winter range at 3 spatio-temporal scales: herd range based on 100% minimum convex polygons around deer locations, home range based on 90% kernel density estimates of deer locations, and foraging range based on locations obtained within 2 hours of sunrise or sunset within the boundaries of the home range scale. We assessed habitat use of mule deer using a generalized linear model with a negative-binomial link function. We validated our models with locations from an independent dataset of 95 deer that wintered within 8 of our analysis areas. Model validation indicated that regional models for all spatio-temporal scales predicted probability of use moderately to very well. At all spatio-temporal scales, predicted use by mule deer was greater in areas with forest canopy cover. These findings call into question large-scale removal of western juniper (*Juniperus occidentalis*) in Oregon and other portions of western United States to enhance habitat for sagebrush-dependent wildlife species. Across all spatio-temporal scales, we documented increased probability of use of areas farther from roads open to motorized vehicle use by mule deer, highlighting the importance of limiting motorized vehicle use and access on mule deer winter range. We also documented increased use of areas with lower snow depth and on moderate slopes by mule deer. Our models can be used in land management planning to spatially predict mule deer distribution and probability of use under alternative management scenarios that affect forest canopy cover or motorized vehicle use on roads while accounting for other physical features of the landscape. Additionally, our models can be used to develop juniper removal projects to mitigate effects on mule deer winter range habitat while benefiting other wildlife. © 2018 The Wildlife Society.

KEY WORDS habitat use, juniper, *Juniperus occidentalis*, mule deer, multiscale, *Odocoileus hemionus*, Oregon, roads, winter range.

Mule deer (*Odocoileus hemionus hemionus*) populations throughout the western United States have experienced

decades-long population fluctuations over the past century (Wallmo 1981, Unsworth et al. 1999), including populations in Oregon (Cliff 1939, Ebert 1976, Salwasser 1979, Peek et al. 2002). Mule deer populations in Oregon peaked at approximately 575,000 in the 1960s (Workman and Low 1976) and declined to nearly 230,000 by early 2015 (Oregon Department of Fish and Wildlife [ODFW] 2003; ODFW, unpublished data). Several hypotheses have been proposed to explain population declines of mule deer (Ballard et al. 2001, Peek et al. 2001, Hurley et al. 2011, Shallow et al. 2015, Johnson et al. 2017). One compelling argument is that

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Table 3. Home range coefficients for analysis areas in models of mule deer habitat use during winter in south-central Oregon and northern California, USA, 2006–2012. Regional estimates are the geometric mean of coefficients from individual analysis areas.

Analysis area	Intercept	Proportion forest	Proportion forest ²	Mean snow depth (cm)	Slope (%)	Slope ²	Distance to open road (km)
Metolius	–8.110	1.884	–1.610	–0.006	0.007	–0.000	0.251
North Paulina	–7.782	1.717	–1.002	–0.014	0.030	0.000	–0.781
Wagontire	–9.498	1.566	–1.546	–0.030	0.095	–0.002	0.238
South Paulina	–8.347	0.362	–0.472	–0.001	–0.007	0.000	0.136
Fort Rock	–7.586	1.633	–1.400	–0.001	–0.018	0.000	–0.163
Silver Lake	–8.239	1.826	–1.314	–0.002	–0.034	0.000	–0.054
East Interstate	–8.528	2.476	–2.525	0.002	0.064	–0.001	0.188
West Interstate	–8.878	0.346	–0.347	0.000	0.160	–0.006	0.352
Klamath	–8.398	3.573	–1.817	–0.003	0.006	–0.001	0.097
Regional	–8.374	1.709	–1.337	–0.006	0.034	–0.001	0.029
Lower 95% CI		1.255	–1.715	–0.011	0.003	–0.002	–0.154
Upper 95% CI		2.232	–0.997	–0.001	0.067	–0.000	0.185

($r_s \geq 0.75$) at 1 of 8 analysis areas, moderately correlated ($0.75 > r_s > 0.50$) at 3 analysis areas, and marginally or weakly correlated ($r_s < 0.50$) at 3 analysis areas, and negatively correlated at 1 analysis area (Table S4). Across our 3 spatio-temporal scales of analysis, Wagontire, Silver Lake, and Klamath had consistently high validation scores, whereas Metolius, North Paulina, and Fort Rock had the lowest.

DISCUSSION

Perhaps the primary determinant of distribution of mule deer during winter is snow depth, with depths >46 cm effectively precluding use (Gilbert et al. 1970). Our results supported this conclusion; one of the strongest relationships we observed in our analysis was decreased use of areas with

increased snow depth in the herd range and home range models. This pattern of increased use in areas with decreased snow depth is likely influenced by energy costs and foraging efficiency. For example, increased snow cover and depth reduces forage availability and foraging efficiency of ungulates (Wickstrom et al. 1984). Further, energy expenditure from locomotion increased in a log-linear manner with increased snow depth (Parker et al. 1984). Consequently, it was not surprising that mule deer used areas with lower snow depth within our analysis areas. We did not observe a relationship between snow depth and habitat use by mule deer in our foraging range models. We contend we did not observe this relationship because patterns of habitat use at coarser scales (e.g., herd range and foraging range) already accounted for deer using areas with reduced snow cover.

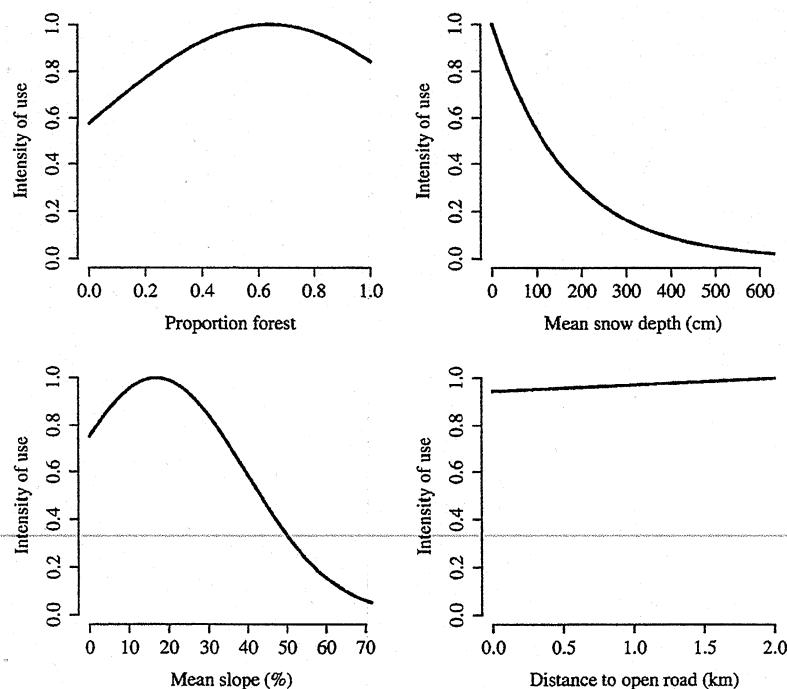


Figure 3. Marginal plots from an analysis of mule deer winter habitat use in south-central Oregon and northern California, USA, 2006–2012. Plots are for the regional home range model and show intensity of use in relation to individual model covariates, when all other covariates included in the model are held at their medians.

Table 4. Foraging range coefficients for analysis area models of mule deer habitat use during winter in south-central Oregon and northern California, USA, 2006–2012. Regional estimates are the geometric mean of coefficients from individual analysis areas.

Analysis area	Intercept	Proportion canopy cover 1–20%	Proportion canopy cover >20%	Slope (%)	Slope ² (%)	Distance to open road (km)	Distance to open road ² (km)
Metolius	–8.221	0.654	0.007	0.003	–0.000	–0.126	0.198
North Paulina	–7.711	0.895	0.565	0.015	–0.000	–0.677	0.004
Wagontire	–9.721	0.426	–0.007	0.090	–0.003	0.795	–0.266
South Paulina	–8.234	0.106	–0.226	0.005	–0.001	–0.519	0.306
Fort Rock	–7.879	0.518	0.197	–0.004	0.000	0.565	–0.334
Silver Lake	–8.389	0.879	0.356	–0.020	0.000	–0.145	0.074
East Interstate	–8.634	0.630	–0.083	0.064	–0.001	0.887	–0.361
West Interstate	–9.823	0.660	0.183	0.170	–0.006	2.295	–0.915
Klamath	–9.421	1.944	1.673	0.021	–0.001	2.015	–0.803
Regional	–8.670	0.746	0.296	0.038	–0.001	0.566	–0.233
Lower 95% CI		0.517	0.041	0.009	–0.003	0.012	–0.459
Upper 95% CI		1.042	0.618	0.074	–0.000	1.149	–0.001

Across our 3 spatio-temporal scales of analysis, we documented several associations between forest cover and habitat use by mule deer. Interpretation of these patterns varied across spatial and temporal scales and likely highlighted the importance of mule deer balancing the needs of thermal and hiding cover with foraging opportunity. At the herd range scale, we documented increased intensity of use by deer in areas closer to forest cover and at the home range scale, increased intensity of use was associated with areas composed of 60–70% forest. We contend this indicates mule deer were using areas at these spatial scales that allowed them to seek thermal or hiding cover. In contrast, at the foraging range scale, we documented increased use of areas

with low forest canopy cover (i.e., 1–20%) and decreased intensity of use of areas with >20% forest canopy cover. Areas with lower canopy cover likely had increased forage because herbaceous understory vegetation decreases substantially where juniper cover is >20% (Miller et al. 2000, Witt and Patterson 2011). The need for shrubs and associated vegetation for forage (Leckenby 1977) and tree cover for thermal and hiding (Leckenby and Adams 1986) necessitates the use of forested and unforested areas during winter (Kie et al. 2002). We contend mule deer in our study area concentrated use in areas that provided sufficient thermal and hiding cover while also providing foraging opportunities in areas with relatively low forest canopy cover (<20%).

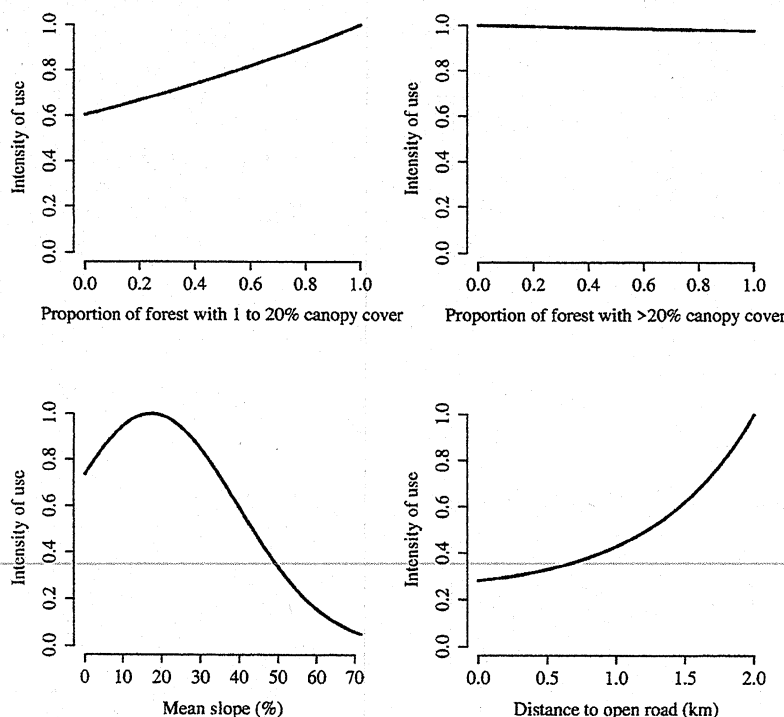


Figure 4. Marginal plots from an analysis of mule deer winter habitat use in south-central Oregon and northern California, USA, 2006–2012. Plots are for the regional foraging range model and show intensity of use in relation to individual model covariates, when all other covariates included in the model are held at their medians.

412, 500 ac!

Forest cover is an important component of mule deer winter habitat use throughout the inter-mountain west in Colorado, Oregon, Washington, British Columbia, and Idaho (Leckenby and Adams 1986, Carson and Peek 1987, D'Eon and Serrouya 2005, Anderson et al. 2012, Smith et al. 2015). Perhaps the most compelling function of forest cover is that it provides important energetic benefits for mule deer. Because of their low ratio of body mass to surface area, mule deer have a small thermal neutral zone and may have increased needs for thermal cover, particularly during winter (Raedeke and Taber 1982). Consequently, mule deer in our study likely used forest cover to regulate body temperature during cold winter conditions (Leckenby and Adams 1986). Further, forest canopy intercepts snowfall and influences snow accumulation patterns so that snow depth is lower in forested areas (Pomeroy et al. 1998). Mule deer use areas with forest cover to mediate effects of snow (Mysterud and Østbye 1999) and this pattern was present in our study area.

Predation is often a proximate cause of mortality in mule deer populations (Bleich and Taylor 1998, Ballard et al. 2001, Forrester and Wittmer 2013) and forest cover may be used by mule deer in an effort to reduce risk of predation (Mysterud and Østbye 1999). For example, forest cover may allow increased concealment and escapement from predators (Bowyer and Bleich 1984, Jedrzejewska et al. 1994). Consequently, minimization of predation risk may be an alternative or supplemental explanation to the patterns we documented of increased use of forest cover by mule deer on winter range. However, we lacked data on mule deer predators within our study areas to test this hypothesis, so we can not explicitly link use of forest cover to reduced predation risk.

In our analysis areas, western juniper was the primary tree species and given our associations between mule deer habitat use and forest cover, juniper is likely an important habitat feature for mule deer winter range. Western juniper has been expanding within shrub-steppe communities in Oregon since 1900 (Miller and Rose 1999). In Oregon, juniper removal has occurred on >165,000 ha from 2010–2015 in efforts to benefit sage-grouse (*Centrocercus urophasianus*; Natural Resources Conservation Service 2015, Sage-Grouse Conservation Partnership 2015) and other sagebrush-dependent species; however, evidence to support any positive or detrimental benefits of juniper removal on mule deer habitat use or demography is lacking. Leckenby (1978) suggested that clear-cutting juniper on winter range could be detrimental to mule deer because thermal and hiding cover would be removed. Increases in juniper cover across mule deer winter range, however, may have negatively affected forage availability for mule deer because abundance of shrubs, forbs, and grasses decline in juniper stands (Miller et al. 2000, Peek et al. 2001). Past research has indicated that nutritional resources during winter can influence survival and population dynamics of mule deer (Baker and Hobbs 1985, Bishop et al. 2009, Bergman et al. 2014) and if increases in juniper cover have reduced forage quantity and quality for mule deer, this could have population-level consequences. Given the lack of knowledge on effects of juniper treatments on mule deer habitat use and demography,

future research to elucidate effects of juniper removal on mule deer is warranted.

One of the strongest patterns we observed across all 3 spatio-temporal analyses was a consistent avoidance of roads open to motorized vehicle use, which has also been documented in Wyoming, Colorado, and southeast Alaska (Sawyer et al. 2006, Webb et al. 2013, Northrup et al. 2015, Gilbert et al. 2017). In contrast, in Idaho, where mule deer shared winter range with elk, mule deer were closer to roads during winter, whereas elk used areas farther from roads (Stewart et al. 2010). This pattern likely occurs because of competitive interactions between the mule deer and elk, where mule deer are displaced by elk to areas closer to roads (Johnson et al. 2000). In our analysis areas, no or very few elk co-occurred with mule deer on winter range (ODFW, unpublished data), which allowed us to establish clearer inference regarding effects of roads open to motorized vehicle use on mule deer winter habitat use. In other areas, ungulates demonstrated avoidance of roads open to motorized access and open areas (e.g., meadows, non-forest) during the day but used areas closer to both at increased frequencies at night (Ager et al. 2003, Crosmarty et al. 2012, Bonnot et al. 2013, Northrup et al. 2015). Given the associations we documented between use of forest cover and habitat use by mule deer, forest cover may be used by mule deer to minimize the effects of human disturbance in our study areas. Forest cover allows increased concealment and escape-ment from human hunting (Kufeld et al. 1988) and minimization of disturbance from other forms of human recreation (Wisdom et al. 2004), which aligns with our findings that mule deer spent less time in areas close to roads open to motorized vehicle use.

We view our findings of mule deer avoidance of roads open to motorized vehicle use to be linked to human disturbance, and not the physical features of the road. The strong avoidance of roads open to motorized vehicle use, and associated human disturbance, by ungulates observed in our study and others (Rowland et al. 2000, Sawyer et al. 2006, Coe et al. 2011, Webb et al. 2013, Gilbert et al. 2017) suggests a substantial portion of what may be suitable habitat may no longer be used (Rogala et al. 2011). In a meta-analysis of the effects of flight responses of ungulates to human disturbance, it was found that ungulates, including mule deer, had a strong avoidance and increased movement rates in response to human activity, especially for hunted populations (Stankowich 2008) like our study populations in south-central Oregon. Consequently, human disturbance associated with motorized vehicle use on roads may cause mule deer to increase movement rates, leading to a net reduction in their energy budget, which could ultimately have demographic consequences (Robinette et al. 1973, Bishop et al. 2009, Tollefson et al. 2010). Fortunately, given that ungulates likely respond to the disturbance associated with motorized vehicle use of roads and not the road itself, this situation can be rectified through seasonal or permanent road closures. Finally, increased densities of roads open to motorized vehicle use are likely to increase human access and rates of poaching (Cole et al. 1997). In our study areas, poaching represented 3.1% of adult female mule deer

mortality (Mulligan 2015). Population growth rates of ungulates are highly sensitive to changes in adult female survival (Gaillard et al. 1998, 2000) and the rate of poaching observed in our study areas could be contributing to reductions in population growth rates.

At all 3 of our spatio-temporal analysis scales, we observed a strong association of mule deer using areas of moderate (10–30%) slopes and at the herd range scale showed a weak relationship with increased use on northern aspects. Prevailing winter winds in our analysis areas were from the south and deer typically seek shelter from wind when gusts are >40 km/hour and temperatures <−10°C (Loveless 1967, Wood 1988). Topography can effectively serve as thermal cover for deer by providing a windbreak. Most of our analysis areas were relatively flat ($\bar{x}$ slope across the 9 analysis areas was 8.4%) and we contend deer increased use on northern aspects and moderate slopes within our analysis areas as protection from wind, given the scarcity of topographic complexity on the landscape.

Our overarching objective was to assess habitat use patterns of mule deer across multiple analysis areas to document habitat use patterns on a regional scale. Using this approach, our regional models were able to accurately predict habitat use in most analysis areas and we identified several robust patterns of habitat use of mule deer on winter range that are informative to managers. Despite the benefits of our modeling approach, validation results across our 3 spatio-temporal scales and 9 individual analysis areas were not perfect. There are several possible reasons for poor validation results in any particular analysis area: difference in physiographic characteristics, differences in the proportion of shrub or other covariates, or small validation sample sizes. No one reason stands out among these options. The most likely explanation for low correlation between predicted and observed use in any of the analysis areas is that predictor variable(s) important at an individual analysis area scale were not identified prior to our modeling efforts or were not included in the regional model. Given the geographic area and diversity of conditions experienced by mule deer in our analysis areas, this was not unexpected, and it highlights the complexity of modeling habitat use patterns for species across large areas.

MANAGEMENT IMPLICATIONS

We encourage wildlife and land managers to employ predictive models developed here and other areas in a GIS to assess effects of proposed management actions such as timber harvest, juniper removal, or closures of roads open to motorized vehicle use in mule deer winter range. These models and models developed elsewhere for mule deer will allow effective assessment of alternative management practices such as habitat treatments and changes to motorized vehicle access to quantify the degree to which management practices may be beneficial or detrimental.

Our models identified 2 robust patterns of mule deer winter habitat use that are under direct influence of land managers: increased use of areas with forest cover and decreased use of areas with roads open to motorized vehicle access. We

encourage land managers to implement permanent or seasonal road closures on mule deer winter range to minimize disturbance and displacement of mule deer. We also recommend managers attempt to retain forested areas within mule deer winter ranges to increase use by mule deer. Based on our results showing an association between forest cover and winter habitat use by mule deer, habitat management that benefits species such as sage-grouse (e.g., widespread juniper removal) have the potential to reduce use of these areas by mule deer during winter. Consequently, we recommend managers implement projects that consider and integrate the needs of multiple species. For example, where mule deer and sage-grouse co-occur, mitigation of effects of removal of tree cover to benefit sage-grouse could occur through strategic planning to minimize vegetation disturbance in areas that have other attributes associated with increased probability of use by mule deer but not of sage-grouse (e.g., moderate slopes). Consideration of multiple vegetation treatment prescriptions (e.g., thinning vs. complete juniper removal) will also allow managers to identify alternative management practices that mitigate or benefit predicted habitat use by mule deer in conjunction with balancing the needs of other sagebrush-dependent species. Although snow depth is a factor outside the control of wildlife managers, our models could be used to identify areas that have a high probability of use by mule deer during winters with heavy snowfall. During these years, mule deer populations are likely to be nutritionally stressed and have increased risk of overwinter mortality. Our models can be used to identify these areas and assign a high level of protection from future land management changes to ensure the long-term conservation of mule deer winter range.

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Farmington Daily Times

NEWS

'Hundreds of thousands, if not millions': New Mexico sees massive migratory bird deaths

Algernon D'Ammassa Las Cruces Sun-News

Published 2:41 p.m. MT Sep. 12, 2020 | Updated 2:56 p.m. MT Sep. 12, 2020

LAS CRUCES - Biologists from New Mexico State University and White Sands Missile Range examined nearly 300 dead migratory birds Saturday at Knox Hall on the university's main campus.

Over the past few weeks, various species of migratory birds are dying in "unprecedented" numbers of unknown causes, reported Martha Desmond, a professor at NMSU's Department of Fish, Wildlife and Conservation Ecology.

"It is terribly frightening," Desmond said. "We've never seen anything like this. ... We're losing probably hundreds of thousands, if not millions, of migratory birds."

In August, large numbers of birds were found dead at White Sands Missile Range and at the White Sands National Monument in what was thought to be an isolated incident, Desmond said.

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After that, however, came reports of birds behaving strangely and dying in numerous locations in Doña Ana County, Jemez Pueblo, Roswell, Socorro and other locations statewide.

The affected birds have included warblers, sparrows, swallows, blackbirds, flycatchers, and the western wood pewee.

"A number of these species are already in trouble," Desmond said. "They are already experiencing huge population declines and then to have a traumatic event like this is – it's devastating."

On Saturday, Desmond was joined by Trish Cutler, a wildlife biologist at WSMR, and two NMSU students for an initial evaluation of the carcasses.

Desmond said her team also began catching and evaluating living specimens on Friday as residents find birds behaving strangely and gathering in large groups before dying.

"People have been reporting that the birds look sleepy ... they're just really lethargic," Cutler said. "One thing we're not seeing is our resident birds mixed in with these dead birds. We have resident birds that live here, some of them migrate and some of them don't, but we're not getting birds like roadrunners or quail or doves."

On the other hand, numerous migratory species are dying rapidly and it is not immediately clear why, although the cause appears to be recent. Desmond said the birds had moulted, replacing their feathers in preparation for their flight south, "and you have to be healthy to do that; but somewhere after that, as they initiated their migratory route, they got in trouble."

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The biologists guessed the cause might involve the wildfires ravaging the western U.S. and dry conditions in New Mexico.

"They may have been pushed out before they were ready to migrate," Desmond said. "They have to put on a certain amount of fat for them to be able to survive the migration. These birds migrate at night and they get up in the jet stream, and they might migrate for three nights in succession, they'll come down and they'll feed like crazy, put on more fat and go again."

The biologists noted that the majority of the dying birds are insectivores, but that seed eaters were sickening and dying as well.

The birds will be sent to the U.S. Fish and Wildlife Service Forensics Laboratory in Ashland, Ore. for further analysis. Desmond it could be weeks before results come back, and the findings could bear serious ecological implications.

"Over 3 billion birds have died since 1970. Insect populations are crashing, and this is just an unprecedented mortality," she said. "Climate change is affecting the abundance of insects, it's affecting the volatility of the fires, and the scary thing is this may be an indication of the future."

9/16/2020

Birds are mysteriously dying in New Mexico in 'frightening' numbers

Algernon D'Ammassa can be reached at 575-541-5451, adammassa@lcsun-news.com or @AlgernonWrites on Twitter.

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GREATER SAGE-GROUSE

*Ecology and Conservation
of a Landscape Species and Its Habitats*

Steven T. Knick and John W. Connelly, *Editors*

Studies in Avian Biology No. 38

2011

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CHAPTER SEVENTEEN

Influences of Environmental and Anthropogenic Features on Greater Sage-Grouse Populations, 1997–2007

Douglas H. Johnson, Matthew J. Holloran, John W. Connelly,
Steven E. Hanser, Courtney L. Amundson, and Steven T. Knick

Abstract. The Greater Sage-Grouse (*Centrocercus urophasianus*), endemic to western North America, is of great conservation interest. Its populations are tracked by spring counts of males at lek sites. We explored the relations between trends of Greater Sage-Grouse lek counts from 1997 to 2007 and a variety of natural and anthropogenic features. We found that trends were correlated with several habitat features, but not always similarly throughout the range. Lek trends were positively associated with proportion of sagebrush (*Artemisia* spp.) cover, within 5 km and 18 km. Lek trends had negative associations with the coverage of agriculture and exotic plant species. Trends also tended to be lower for leks where a greater proportion of their surrounding landscape had been burned. Few leks were located within 5 km of developed land and trends were lower for those leks with more developed land within 5 km or 18 km. Lek trends were reduced where communication towers were nearby, whereas no effect of power lines was detected. Active oil or natural gas wells and highways, but not secondary roads, were associated with lower trends. Effects of some anthropogenic features may have already been manifested before our study period and thus not have been detected in this analysis. Results of this

range-wide analysis complement those from more intensive studies on smaller areas. Our findings are important for identifying features that could threaten Greater Sage-Grouse populations.

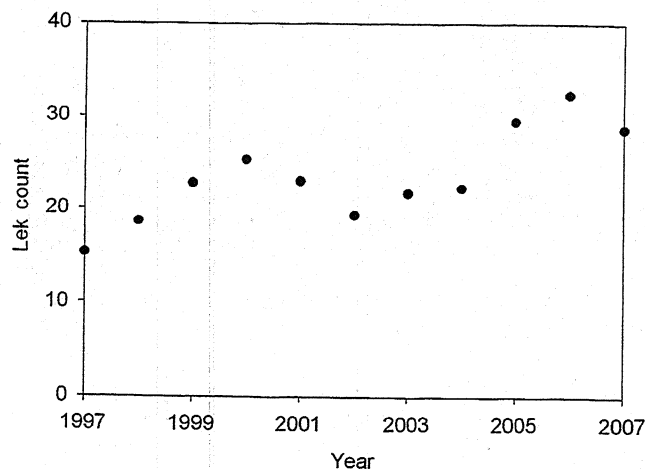
Key Words: *Centrocercus urophasianus*, communication towers, Greater Sage-Grouse, lek, oil and gas wells, population, roads, sagebrush.

Influencias de Características Ambientales y Antropogénicas en Poblaciones de *Centrocercus urophasianus*, 1997–2007

Resumen. El Greater Sage-Grouse (*Centrocercus urophasianus*) es endémico a Norteamérica occidental y de gran interés para la conservación. Sus poblaciones son monitoreadas mediante conteos de los machos en los sitios donde se encuentran los leks (asambleas de cortejo) en la primavera. Exploramos las relaciones entre las tendencias de conteos de leks de Greater Sage-Grouse durante 1997–2007 y una variedad de características naturales y antropogénicas. Encontramos que las tendencias estaban correlacionadas con varias características del hábitat, pero no siempre de forma similar en todo el territorio. Las tendencias de los leks estuvieron positivamente asociadas a la

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on Greater Sage-Grouse populations, 1997–2007. Pp. 407–450 in S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, CA.

Figure 17.2. Average counts during 1997–2007 for 854 leks that had complete records for that period, across all management zones.



(Table 17.2). Relations in all SMZs but the Great Plains were positive. The Wyoming Basin appeared to have a peak near 2,100 m (Fig. 17.3), but in the other SMZs patterns continued upward (e.g., Northern Great Basin; Fig. 17.4).

We found no relation between lek trends and average annual precipitation (Table 17.2). Our metric was too general to capture any short-term effects due to either drought or deluge. Extremes of drought and deluge, especially on a more local scale, likely have more important consequences to sage-grouse reproduction and survival than does a simple long-term average.

Land Cover

Sagebrush

Sagebrush was common in all SMZs, of course, but least common in the Colorado Plateau, Great Plains, and Columbia Basin and most common in the Northern Great Basin (Table 17.1). The type of sagebrush cover also varied by SMZ. Of note is that the average percentage cover of sagebrush within 5 km exceeded the average within 18 km (Table 17.1), suggesting that sage-grouse leks are preferentially located within sagebrush. Lek trends across all SMZs increased modestly but steadily with the cover of tall sagebrush (combined categories for big sagebrush shrubland, big sagebrush steppe, mountain big sagebrush) at both 5-km (Fig. 17.5) and 18-km (Fig. 17.6) radii (Table 17.2). Patterns within individual SMZs generally were similar, except in

the Columbia Basin and the Colorado Plateau, where data were minimal. Similarly, lek trends across all SMZs increased modestly but steadily with the cover of all sagebrush (combined categories for tall sage and low sagebrush) at both 5-km (Fig. 17.7) and 18-km (Fig. 17.8) radii (Table 17.2).

Low sagebrush was present in all SMZs but the Great Plains. There was no consistent pattern for all SMZs combined (Fig. 17.9), and results for 5- and 18-km radii were similar. Low sagebrush was fairly common in the Northern Great Basin, where trends in lek counts generally increased until the cover of low sagebrush was about 40% of the landscape, after which trends were roughly steady (Fig. 17.10).

Grassland

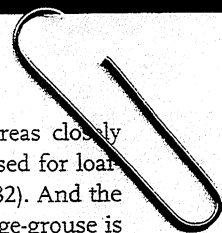
Grassland was common only in the Great Plains, where a slight positive relation could be seen (Fig. 17.11). The Columbia Basin also contained large areas of grassland but had too few leks to draw any conclusions.

Exotic Vegetation

Average cover of exotic vegetation was about 2–3% for all SMZs except the Great Plains and Colorado Plateau, where it was lower (Table 17.1). Lek trends tended to be lower as the cover of exotic species increased at both 5-km (Fig. 17.12) and 18-km scales, although few leks had >8% coverage within either 5 km or 18 km.

TABLE 17.1
Average values of lek count trend, environmental features, and anthropogenic variables, by Sage-Grouse Management Zone (SMZ).

Great Plains	Wyoming Basin	Southern Great Basin	Snake River Plain	Northern Great Basin	Columbia Basin	Colorado Plateau
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Regardless of whether sage-grouse populations increased or decreased during our study period, the analytical techniques we used compared relative patterns, for example, how numbers at leks with towers nearby changed in comparison to leks without nearby towers. Given the consistent effects of prevailing conditions, the relative patterns established across the large number of and broad spatial distribution of leks investigated suggest relationships that were essentially standardized for these prevailing conditions.

Physical Attributes, Land Cover, and Fire History

The distribution of sage-grouse is closely aligned with the distribution of sagebrush-dominated landscapes (Schroeder et al. 2004). The well-documented dependence of the species on sagebrush cannot be overemphasized (Patterson 1952, Connelly et al. 2000c, Hagen et al. 2007). Lek trends across the range of the species were positively associated with the proportions of tall-stature sagebrush and all sagebrush land covers within 5- and 18-km radii of the lek location. Also, the coverage of sagebrush was greater within 5 km than within 18 km. Low sagebrush was common in only the Northern Great Basin SMZ, where it was positively associated with sage-grouse. Walker et al. (2007a) found strong support for models relating lek persistence in southern portions of the Great Plains SMZ with the proportion of sagebrush habitat within 6.4 km. Aldridge et al. (2008) predicted that across the range of the species areas where sage-grouse persisted, compared with areas where populations were extirpated, were those containing at least 25% sagebrush cover within 30 km. Clearly, sagebrush at both local and landscape scales is a necessary, if not sufficient, requirement for viable sage-grouse populations.

Sage-grouse depend on sagebrush through all seasonal periods. Females consistently select areas with more sagebrush canopy cover than other available locations during nesting (Sveum et al. 1998b, Holloran et al. 2005, Hagen et al. 2007), and increased shrub cover at nests has been linked to increased probability of a successful hatch (Wallestad and Pyrah 1974, Gregg et al. 1994). Sage-grouse broods throughout Wyoming selected relatively dense sagebrush stands between hatching and 2 weeks post-hatching, presumably for thermal and predator protection of young chicks (Thompson et al. 2006). During

summer, sage-grouse select mesic areas closely associated with sagebrush that are used for loafing and security cover (Klebenow 1982). And the primary requirement of wintering sage-grouse is sagebrush exposure above the snow (Patterson 1952, Hupp and Braun 1989, Crawford et al. 2004); winter ranges in general are characterized by large expanses of dense sagebrush (Eng and Schladweiler 1972, Beck 1977).

Lek trends were positively related to elevation in the northwestern portion of sage-grouse range. The positive relation was consistent over all elevations in the Northern Great Basin and at elevations greater than average in the Snake River Plain and Columbia Basin SMZs. These SMZs have lower mean lek elevations (Table 17.1). The risk of invasion by exotic annual grasses such as cheatgrass in big sagebrush communities is greatest at lower-elevation (<1,500 m), drier sites (Hemstrom et al. 2002, Crawford et al. 2004). Because of shortened fire-return intervals and the inability of sagebrush-steppe plant communities to recover from fire quickly, invasion of a sagebrush-dominated site by annual grasses may result in the permanent conversion of that site into one that is unsuitable for sage-grouse (d'Antonio and Vitousek 1992, Brooks et al. 2004a, Baker 2006a). Although SMZs differed little in the average proportional area dominated by exotic vegetation (Table 17.1), few leks across the range of the species had >8% cover within 5 km or 18 km, suggesting that when the extent of the landscape dominated by exotic vegetation becomes relatively high, leks become inactive (Enyeart 1956; Connelly et al. 2000c; Miller et al., this volume, chapter 10).

The functional conversion of relatively small amounts of landscape either through exotic species invasion or agricultural conversion had pronounced negative effects on sage-grouse populations. Lek count trends tended to be more negative for leks with greater proportions of either exotic species or agricultural land cover, even at low proportions. Extirpation of sage-grouse throughout the species' range was found to be most likely in areas that had >25% cultivated cropland within 30 km (Aldridge et al. 2008). Inactive sage-grouse leks were noted to have a higher percentage of tillage agriculture within 4 km and within 6.4 km compared with active leks in eastern (Smith 2003) and southern portions of the Great Plains (Walker et al. 2007a). Additionally, replacement of native understory vegetation by exotic annual grasses such as cheatgrass has altered fire regimes, resulting in

losses of sagebrush over large expanses of the Southern Great Basin, Snake River Plain, Northern Great Basin, and the Columbia Basin SMZs (Mack 1981, Knick and Rotenberry 1997, Wambolt et al. 2002, Crawford et al. 2004, Beck et al. 2009).

Greater Sage-Grouse populations have consistently responded negatively to habitat management practices that manipulated large proportions of sagebrush on a landscape (Connelly et al. 2000c). We found that lek count trends across the range of the species generally were lower the greater the area burned within 5 km and 18 km. No relationship was evident between number of post-fire years and lek count trends, however. Baker (2006a) reports that the time required to burn once through an area in big sagebrush-dominated habitats is >70 years, indicating that the 11 years of our analysis was inadequate to determine long-term effects of fire on sage-grouse populations.

In most SMZs, sage-grouse lek trends tended to be higher at higher elevations. Exceptions were the Great Plains, with no consistent trend, and the Wyoming Basin, where a peak at about 2,000 m was evident. This association may reflect the greater human development and disturbances associated with valleys in mountainous areas.

We found no consistent relationship between lek count trends and mean precipitation across SMZs. However, our study period may be too short to identify potential long-term effects of precipitation on populations. Severe, persistent drought conditions have coincided with declining sage-grouse populations throughout the range of the species both historically (1930s) and recently (mid-1980s to early 1990s) (Patterson 1952, Connelly and Braun 1997, Aldridge et al. 2008), and researchers have surmised that grouse numbers were reduced during periods of below-average precipitation (Slater 2003, Holloran et al. 2005, Moynahan et al. 2007). Mean annual precipitation by states throughout the species' range suggests that below-average conditions have persisted for one to four ($\bar{x}$ = 1.7) consecutive years since 1960. Our use of mean precipitation during the 11-year period did not allow us to explore any short-term effects of annual precipitation on sage-grouse populations.

Anthropogenic Features

Sage-grouse populations and distributions in many areas have diminished as a result of modifications to sagebrush-dominated landscapes from anthro-

pogenic activities (Connelly et al. 2000c, Knick et al. 2003). Few sage-grouse leks were located within 5 km of developed land, and a strong negative relationship was found between lek count trends and the proportion of the landscape developed within 5 km or 18 km. Many of the anthropogenic stressors associated with urban and suburban areas may act synergistically to cause sagebrush habitat fragmentation (Knick et al. 2003, Leu et al. 2008). As a landscape becomes bisected into smaller patches of habitat, functional connectivity among patches may be lost (With and Crist 1995). A patch of habitat that by itself is too small to support sage-grouse may nonetheless be valuable to the species if it is connected to other patches of suitable habitat. If that connection is lost, the patch may no longer have value (Fahrig 2003). Viable sage-grouse populations require large landscapes (Patterson 1952, Connelly et al. 2000c), so fragmentation resulting even from scattered disturbances may lead to disproportionate population declines or regional extinctions.

Lek count trends tended to be lower on leks that had >20 km of interstate, federal, or state highway within 18 km and on leks nearer such highways, but no apparent relationship occurred between lek count trends and the presence of secondary roads. Avoidance of roads by Greater Sage-Grouse (Lyon and Anderson 2003), Gunnison Sage-Grouse (Oyler-McCance 1999), and Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*; Crawford and Bolen 1976, Hagen 2003) has been documented. Given that most major highways were constructed before 1997, their major effects likely occurred before our study period, and leks near highways that have persisted may be situated where topography has isolated them from these sources of disturbance (Braun et al. 2002). However, declines in count trends during the study period suggest a continuing disturbance associated with highways, possibly due to increased traffic levels, which have been identified as reducing numbers of sage-grouse occupying leks (Remington and Braun 1991, Holloran 2005).

The apparent reaction of sage-grouse to vertical structures at leks varied by the type of structure. Lek count trends were negatively related to proximity to the closest communication tower and to the number of towers within 18 km. However, trends were not consistently related to the distance to nearest power line or to the length of power line within 5 km or 18 km. Towers typically indicate

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Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forests

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Abstract: During the two breeding seasons immediately following the numerous and widespread fires of 1988, I estimated bird community composition in each of 34 burned-forest sites in western Montana and northern Wyoming. I detected an average of 45 species per site and a total of 87 species in the sites combined. A compilation of these data with bird-count data from more than 200 additional studies conducted across 15 major vegetation cover types in the northern Rocky Mountain region showed that 15 bird species are generally more abundant in early post-fire communities than in any other major cover type occurring in the northern Rockies. One bird species (Black-backed Woodpecker, *Picoides arcticus*) seems to be nearly restricted in its habitat distribution to standing dead forests created by stand-replacement fires. Bird communities in recently burned forests are different in composition from those that characterize other Rocky Mountain cover types (including early-successional clearcuts) primarily because members of three feeding guilds are especially abundant therein: woodpeckers, flycatchers, and seedeaters. Standing, fire-killed trees provided nest sites for nearly two-thirds of 31 species that were found nesting in the burned sites. Broken-top snags and standing dead aspens were used as nest sites for cavity-nesting species significantly more often than expected on the basis of their relative abundance. Moreover, because nearly all of the broken-top snags that were used were present before the fire, forest conditions prior to a fire (especially the presence of snags) may be important in determining the suitability of a site to cavity-nesting birds after a fire. For bird species that were relatively abundant in or relatively restricted to burned forests, stand-replacement fires may be necessary for long-term maintenance of their populations. Unfortunately, the current fire policy of public land-management agencies does not encourage maintenance of stand-replacement fire regimes, which may be necessary for the creation of conditions needed by the most fire-dependent bird species. In addition, salvage cutting may reduce the suitability of burned-forest habitat for birds by removing the most important element—standing, fire-killed trees—needed for feeding, nesting, or both by the majority of bird species that used burned forests.

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Composición de las comunidades de aves luego del reemplazo de rodales a causa de incendios forestales en bosques de coníferas de las montañas Rocosas del norte

Resumen: Durante las dos últimas temporadas de cría inmediatamente después de los numerosos y extensos incendios de 1988, estimé la composición de la comunidad de aves en cada uno de los sitios de bosques incendiados, en el oeste de Montana y el norte de Wyoming. Detecté un promedio de 45 especies por sitio y un total de 87 especies en todos los sitios combinados. Una recopilación de estos datos con otros de conteo de aves a partir de más de 200 sitios adicionales, conducido a lo largo de 15 tipos principales de cobertura de vegetación en las montañas Rocosas del norte mostró que 15 especies de aves eran en general más abundantes en las comunidades tempranas posteriores al incendio, que en cualquier otro tipo principal de cobertura presente en las Rocosas del norte. Una especie de ave (el pájaro carpintero de espalda negra, *Picoides arcticus*) parece estar restringida en su distribución a los árboles muertos en pie, que quedan a causa del reemplazo de rodales a partir de los incendios. Las comunidades de aves en los bosques recientemente incendiados, son diferentes en composición de aquellos que caracterizan otros tipos de cobertura de las montañas Rocosas (in-

Table 4. The numbers of seven species of conifers (>10 cm diameter at breast height) encountered along a series of transects in the Grant Village, North Fork, Canyon Creek, and Blackfoot-Clearwater sites, and the percentages of those used by woodpeckers for feeding purposes.

Tree Species	(n)	Woodpecker use (%)*
Ponderosa pine, <i>Pinus ponderosa</i>	297	80.5
Western larch, <i>Larix occidentalis</i>	100	64.0
Douglas-fir, <i>Pseudotsuga menziesii</i>	593	47.9
Engelmann spruce, <i>Picea engelmanni</i>	109	2.3
Lodgepole pine, <i>Pinus contorta</i>	647	0.2
Subalpine fir, <i>Abies lasiocarpa</i>	172	0.0

*Percentages differ significantly among tree species ($G = 1081$, $p = 0.000$).

species are not the same as those that best predict the presence of another. Accordingly, the single variable that shows the best partial correlation with bird abundance varies widely among species (Table 7).

Discussion

Contrary to what one might expect to find immediately after a major disturbance event, I detected a large number of species in forests that had undergone stand-replacement fires. Huff et al. (1985) also noted that the density and diversity of bird species in one- to two-year-old burned forests in the Olympic Mountains, Washington, were as great as in adjacent old-growth forests. These numbers are not an artifact of birds simply passing through on their way from one adjacent unburned area to another. Most species we detected were feeding in the burned forests, and at least a third (36%) of those detected were nesting therein as well. If the birds were merely feeding while passing through, I should have detected more species and individuals in small burns and fewer in large burns because the probability of passage should decrease with increased isolation from unburned source areas. In fact, the presence of a species was

Table 6. Number (%) of cavity and open-cup nests in each of six classes of potential nest sites.

Nest Site	Cavity Nests	Open-Cup Nests	Available (%)*
Broken-Top Conifer	15 (31)	3 (14)	6
Intact-Top Conifer	12 (25)	9 (44)	92
Broken-Top Aspen	2 (4)	0 (0)	0
Intact-Top Aspen	18 (38)	0 (0)	2
In Bank, On Ground	1 (2)	8 (38)	n/a
In Shrub	0 (0)	1 (5)	n/a

*Based on a sample of 200 trees along a single, 10-m-wide transect in the Canyon Creek site.

largely independent of burn size; in only two cases (Townsend's Solitaire [*Myadestes townsendi*] and Solitary Vireo [*Vireo solitarius*]) was bird abundance significantly negatively correlated with burn size, and those species may indeed have been present in the smaller burns because of the proximity of unburned forest to some of the census points.

Several bird species seem to be relatively restricted in distribution to early post-fire conditions. These include Olive-sided Flycatcher, Three-toed Woodpecker, Black-backed Woodpecker, Clark's Nutcracker [*Nucifraga columbiana*], and Mountain Bluebird [*Sialia currucoides*]. Although none of these species may be considered an early post-fire obligate in the strictest sense, few strict obligates are associated with any habitat (Niemi & Probst 1990). I believe it would be difficult to find a forest-bird species more restricted to a single vegetation cover type in the northern Rockies than the Black-backed Woodpecker is to early post-fire conditions. Although it is possible that Black-backed Woodpecker populations are maintained by source refuges of low numbers in unburned forests, it is equally likely that their populations are maintained by a patchwork of recently burned forests. The relatively low numbers in unburned forests may be sink populations that are maintained by birds that emigrate from burns when conditions become less suitable 5-6 years after a fire.

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Table 5. The sizes of each of three species of trees used by woodpeckers for feeding purposes in the Blackfoot-Clearwater site.

Tree Status	Tree Diameter at Breast Height (cm)					Significance*
	0-10	10-20	20-30	30-40	>40	
Douglas-fir, <i>Pseudotsuga menziesii</i>						
not fed upon	269	180	77	9	0	
fed upon	10	70	123	24	10	0.0000
Ponderosa pine, <i>Pinus ponderosa</i>						
not fed upon	261	39	17	1	1	
fed upon	72	175	48	7	9	0.0000
Western Larch, <i>Larix occidentalis</i>						
not fed upon	16	4	0	0	0	
fed upon	11	30	3	0	0	0.0001

*Based on G-test of independence between tree size and signs of feeding activity.

Table 7. Statistical results (*p* values) from analyses of bird communities following fire in conifer forests.

Species ^a	Variation among Sites		Burn Size ^d	Best Correlate ^e
	Abundance ^b	Occurrence ^c		
Red-tailed Hawk	0.164	0.293	-0.015	fire intensity (-)
American Kestrel	0.865	0.958	0.334	fire intensity (-)
Calliope Hummingbird	0.037	0.830	-0.134	larch cover
Williamson's Sapsucker	0.000	0.646	0.110	fir-cedar cover
Hairy Woodpecker	0.003	0.003	-0.362	fire intensity (-)
Three-toed Woodpecker	0.000	0.000	0.193	larch cover
Black-backed Woodpecker	0.003	0.006	0.237	number of small trees
Northern Flicker	0.000	0.000	-0.053	number of small trees
Olive-sided Flycatcher	0.000	0.000	0.276	ground cover
Western Wood-Pewee	0.000	0.000	-0.210	deciduous tree cover
Hammond's Flycatcher	0.043	0.080	-0.106	shrub cover
Dusky Flycatcher	0.000	0.000	-0.122	deciduous tree cover
Tree Swallow	0.000	0.000	0.499*	number of small trees
Gray Jay	0.000	0.151	-0.105	Douglas-fir cover
Steller's Jay	0.000	0.000	-0.089	subalpine fir cover
Clark's Nutcracker	0.000	0.000	0.088	ground cover (-)
Common Raven	0.000	0.000	0.198	fir-cedar cover (-)
Black-capped Chickadee	0.017	0.175	-0.008	spruce cover (-)
Mountain Chickadee	0.000	0.000	0.196	shrub cover (-)
Red-breasted Nuthatch	0.000	0.000	-0.337	lodgepole cover (-)
House Wren	0.000	0.000	-0.219	fir-cedar cover
Ruby-crowned Kinglet	0.000	0.000	0.004	subalpine fir cover (-)
Mountain Bluebird	0.000	0.000	0.032	fire intensity
Townsend's Solitaire	0.000	0.000	-0.430*	spruce cover (-)
Swainson's Thrush	0.000	0.000	-0.140	larch cover
Hermit Thrush	0.000	0.000	-0.079	ponderosa pine (-)
American Robin	0.000	0.000	0.160	number of small trees (-)
Varied Thrush	0.000	0.000	-0.078	subalpine fir cover
Solitary Vireo	0.000	0.023	-0.552**	larch cover
Warbling Vireo	0.000	0.000	0.218	deciduous tree cover
Orange-crowned Warbler	0.001	0.029	-0.284	larch cover
Yellow-rumped Warbler	0.000	0.000	0.339	number of big trees
Townsend's Warbler	0.000	0.014	-0.038	fire intensity (-)
MacGillivray's Warbler	0.000	0.000	-0.132	larch cover
Wilson's Warbler	0.141	0.342	0.240	number of small trees
Western Tanager	0.000	0.000	-0.310	subalpine fir cover (-)
Black-headed Grosbeak	0.000	0.333	0.062	deciduous tree cover
Lazuli Bunting	0.000	0.000	-0.275	ground cover
Chipping Sparrow	0.000	0.000	-0.307	ponderosa pine
Fox Sparrow	0.001	0.045	-0.014	spruce cover
Lincoln's Sparrow	0.001	0.000	0.361	number of big trees
White-crowned Sparrow	0.000	0.000	0.507*	deciduous tree cover
Dark-eyed Junco	0.000	0.000	0.358	number of big trees
Brown-headed Cowbird	0.000	0.000	0.228	subalpine fir cover (-)
Cassin's Finch	0.000	0.000	-0.144	fire intensity
Red Crossbill	0.000	0.000	0.209	deciduous tree cover (-)
Pine Siskin	0.000	0.000	0.114	intensity ^a

^aScientific names given in Table 2.^b*p* value associated with Kruskal-Wallis ANOVA, which was used to test for among-site differences in mean number of individuals per point.^c*p* value associated with G-test, which was used to test for among-site differences in the probability of occurrence.^dPearson rank correlation between mean number of individuals per point and burn size. Asterisk indicates significance at *p* < 0.05, and double asterisk indicates significance at *p* < 0.01. Analyses included only sites with at least five sample points.^eIndependent variable with highest partial correlation from multiple regression that included 13 independent variables.

Detailed studies of movement patterns and demography, needed to resolve this issue, are presently lacking.

In addition to the relative restriction of a few species to early post-fire conditions, many more were simply relatively abundant therein. In the results I note 15 species

(including the five listed above) that were more frequently detected in recently burned forest than in any other cover type available in the northern Rockies. An additional six species (Common Nighthawk [*Chordeiles minor*], Calliope Hummingbird [*Stellula calliope*], North-

ern Flicker [*Colaptes auratus*], Steller's Jay [*Cyanocitta stelleri*], Orange-crowned Warbler [*Vermivora celata*], and Chipping Sparrow [*Spizella passerina*] were most abundant in the slightly older burned forests (10–40 years after fire) (Table 3). Three species (American Robin, Yellow-rumped Warbler [*Dendroica coronata*], and Dark-eyed Junco) were detected in both early- and mid-successional burned forest studies 100% of the time. Thus, burned forests may be of critical importance to a large number of Rocky Mountain bird species that are either relatively restricted to or relatively abundant in such forests.

The picture I paint of bird communities in burned forests contrasts sharply with that painted by other authors (Emlen 1970; Bendell 1974; Lyon et al. 1978; Niemi 1978; Lyon & Marzluff 1985), who have stated that bird communities change little after fire. After a careful review of those papers and the papers that those authors summarized, however, it is clear that the no-effect conclusions have emerged, in part, from studies of low-intensity fires or nonforested habitats and almost always from comparisons of one or two study sites and one or two controls—far too little replication to draw general conclusions about fire effects. Most important, however, the no-effect conclusions are based on composite statistics such as total bird density, species richness, and within-guild abundances, which hide more than they reveal in terms of biological effects of fire on specific species.

Bird species that use burned forests occupy a variety of feeding guilds and most rely heavily on the standing dead trees for food acquisition. For example, several bird species detected in recently burned forests may be taking advantage of the increased availability of conifer seeds after cones open in response to fire. Seed eaters that feed on conifer seeds (especially Clark's Nutcracker, Cassin's Finch [*Carpodacus cassinii*], Red Crossbill [*Loxia curvirostra*], and Pine Siskin [*Carduelis pinus*]) were more abundant in early post-fire habitat than in any other cover type, and they were significantly more abundant (Mann-Whitney $U = 29,568$, $p < 0.001$) in the first year than in the second year following a fire, when conifer-seed resources would have been more depleted. Another feeding group that seems to depend on food provided by the burned trees includes the bark-probing woodpeckers, which eat primarily wood-boring beetles (Beal 1911). Woodpeckers are clearly responding to the increase in availability of cerambycid and buprestid beetle larvae (Evans 1964; Komarek 1969; Bock & Bock 1974; Fellin 1980; Harris 1982; Amman & Ryan 1991), which in some cases are themselves responding to the increase in availability of unburned wood that lies beneath the bark of fire-killed trees (Amman & Ryan 1991). Adult beetles in the genus *Melanophila* are, in fact, specialized to feed on fire-killed trees and are capable of using infrared sensors to detect and colonize

burned forests more than 161 km distant (Evans 1964, 1966). Finally, aerial insectivores (flycatchers, swallows) relied on standing dead trees as perch sites from which they sallied into the open air space for their prey.

Because the pattern of relative bird abundances differed among sites, the relative suitabilities of sites probably also differed among bird species. The same conclusion is suggested by results of the partial correlation analysis, in which the specific elements associated with bird abundance differ among species.

Most (77%) of the bird species I detected in burned forests were migrants. With concern about declining populations of migrants (Askins et al. 1990), perhaps conservation biologists should be devoting more attention to the loss of early successional habitats born of "natural" disturbance by investigating the extent to which such habitats are necessary for the maintenance of viable populations.

Conservation and Management Implications

The Importance of Stand-Replacement Fires

Fires are clearly beneficial to numerous bird species and are apparently necessary for some. The same case has been made for plants, in which some species germinate and flower only within 1–3 years after a fire and then bank their seeds for storage until the next fire (Heinselman 1981). Fire is such an important creator of the ecological variety in Rocky Mountain landscapes (Arno 1980; Gruell 1983) that the conservation of biological diversity is likely to be accomplished only through the conservation of fire as a process. Fire is in fact "... the only natural agent that is sufficiently widespread, abundant, fast, and regular to hold plant successions in seral stages on a vast scale and, therefore, to maintain the diversity of animal life that is so dependent upon such successional vegetation" (Komarek 1966). Efforts to meet legal mandates to maintain biodiversity should, therefore, be directed toward maintaining processes like fire, which create the variety of vegetative cover types upon which the great variety of wildlife species depend (Hansen et al. 1991).

Unfortunately, we are not currently managing the land to maintain the kind of early successional seral stages that follow stand-replacement fires and, hence, many fire-dependent plant and animal species. Why not? First, prescribed fires in conifer forests are most often low-intensity, understory burns that are justified by the argument that, with past fire prevention, forest composition is now "unnatural" and that we need to reintroduce a native fire regime of frequent, mild, understory burns to restore forests and to prevent catastrophic crown fires, which are "destructive" and "unnatural" (Biswell 1968; Alexander & Dube 1982). This justification holds only

for a very limited number of habitat types, however (for example, low-elevation ponderosa pine forests). Most of the forested landscape in the northern Rockies evolved under a regime of high-intensity, large fires every 50–100 years (Fischer & Bradley 1987), not under a regime of low-intensity, frequent understory burns. A study of fire history in the Selway-Bitterroot Wilderness showed that less than 10% of the forested land experienced non-lethal fire; most of the forest types experienced partly to completely lethal fires every 100–200 years (Brown et al. 1994). Although some might argue that all forest types have been subjected to fire suppression for too long and that unnaturally dense understory buildups are leading to unnaturally severe fires, the stand-replacement fires that currently consume forests that evolved under that regime (for example, the 1988 Yellowstone fires) are not at all unusual in intensity or extent (Romme & DeSpain 1989).

Second, current human population and human settlement trends allow for the retention of very few areas large enough to allow free-ranging fire, and almost none of those areas have prescriptions allowing stand-replacement fires to occur (Agee 1991). Even when there is plenty of space to let fires burn, the general response is to expend enormous resources to eradicate fire because of the damage it does to timber resources, the danger it poses to humans and their buildings, and—despite ample evidence to the contrary—the damage it may do to tourism because of the visual impact. Brown and Arno (1991) have addressed this growing predicament of putting fire back into the landscape while still operating within the economic, social, and political constraints that society continues to impose: It will not be easy.

Third, there is a lack of public education about the benefits of stand-replacement fires. The biological naïveté surrounding the 1988 fires was astounding and did more to muster opposition than support for “let it burn” wilderness policies. The lack of understanding demonstrated by the public, especially prominent politicians, generated a good bit of the conflict over policy (Cutler 1988). Simple facts—for example, there exists a strong distributional association between some bird species and burned forests—should be used to garner support from the public for liberal prescribed-fire policies.

Fourth, forests are not being managed in ways that mimic natural processes. One could argue that the loss of burned forest acreage due to fire control has been compensated for, at least in part, by timber harvesting. Many people believe that the conditions present after a clearcut are basically the same as those present after a severe fire (Kohrt 1988; Maschera 1988; Eggleston 1989; Swift 1993). But conditions created by a stand-replacement fire are biologically unique, at least in terms of the biomass of standing, dead trees that remain and, to a much greater extent, in terms of ecosystem structure and function. Clearcutting is, in general, a poor substi-

tute for fire because such timber harvesting does not retain some of the most important elements, such as standing, dead trees, that are integral components of the post-fire ecosystem and that probably contribute to unique successional pathways (Agee 1991; Hansen et al. 1991) and wildlife communities.

Stand-replacement fires should not be viewed as unnatural disasters that can (and should) be prevented (Kipp 1931). As Heinzelman (1985) has argued, plans to maintain stand-replacement fire regimes are justified in at least the more remote of our public lands, and prescribed-fire regimes should not be limited to periodic, mild, understory burning in lower-elevation ponderosa pine forests. Managers must also be careful to mimic all aspects of natural disturbance (such as timing, frequency, and intensity) and not just introduce disturbance as such (Hobbs & Huenneke 1992). Finally, because the pattern of relative bird abundances differs among burns, managers probably need to provide a diversity of burned cover types, intensities, and maybe even a variety in landscape contexts of burns to provide for the variety of species that may depend on fire.

Post-fire Timber Harvesting

On public lands, managers should leave an adequate amount of standing, dead trees after a fire because of the species that depend on that forest element. The current tendency to expedite timber “salvage” sales on burned forest lands needs to be re-examined. Already, as much as 60% of all timber sales on some forests in the Northern Region of the U.S. Forest Service come from salvaged timber (Schwennesen 1992). These sales, which are often exempt from public notice or comment, are generally supported by a well-meaning but misguided public that believes “dead and dying timber ought to be harvested and put to use” (Schwennesen 1992).

If some bird species require burned forests for the maintenance of viable populations (which is strongly suggested by this study), then post-fire salvage cutting may be conducted too frequently to be justified on the basis of sound ecosystem management. In instances where a salvage cut is deemed necessary, managers who wish to mitigate such effects by leaving some of the standing dead trees should be aware that bird species differ in the microhabitats they occupy within a burn. Therefore, methods that tend to “homogenize” the stand structure (such as selective removal of all trees of a certain size and/or species) will probably not maintain the variety of microhabitats and, therefore, bird species that would otherwise use the site. Selective tree removal also generally results in removal of the very tree species (Table 4) and sizes (Table 5) preferred by the more fire-dependent birds. It may be best, instead, to take trees from one part of the burn and leave another part of the burned area untouched. That way, some of the guess-

work associated with choosing what to leave is avoided. This is clearly an area that deserves additional research attention.

Implications for Live-Tree Harvesting Methods

It is unfortunate that the effect of a timber harvesting method on birds (and other vertebrates) is nearly always evaluated in terms of how much the bird community composition changes from before to immediately after harvest (Hutto et al. 1993; Hejl et al. 1995). The method that best mitigates immediate harvest effects (that produces the least change) is generally viewed as the best alternative. Instead, maybe managers should favor methods that minimize deviation not from the bird communities typically associated with the pre-cut forest, but from those associated with the series of post-fire successional communities anticipated to have eventually occurred on that particular plot of land. In this light, many of the "new forestry" thinning practices, which appear favorable in terms of mitigating the immediate effects of cutting, may not represent the best strategy in terms of minimizing the impact of timber harvesting on natural patterns and processes. This is because many of the newer harvesting practices in mid- to high-elevation conifer forests create structurally artificial stands of thinned trees, which may bring "unnatural" combinations of bird species together, eliminate the full range of seral stages, and, perhaps worst of all, reduce the prospect of fire in the future (Gruell 1980). Recent full-page ads by the timber industry in the northern Rocky Mountains (for example, Missoulain, 24 August 1994, p. A-10), have, in fact, emphasized the fire-prevention "benefit" of forest thinning. Such a consequence may be fine at the urban-forest interface. It may be a well-intentioned but misplaced goal, however, for forested wildlands.

Most selective harvesting and thinning methods also result in the loss of large trees, many of which are otherwise destined to become the kind of snags that many primary and secondary cavity nesters depend on for nesting purposes should a stand-replacement fire occur. The predominant use of already existing snags by cavity nesters in burned forests (Table 6) implies that excavation is much easier in those than in the plentiful but otherwise less suitable (sometimes case-hardened) standing, dead trees. Because the most suitable nest trees for cavity excavation are snags that are themselves old-growth elements, one might even suggest that many of the fire-dependent, cavity-nesting birds depend not only on forests that burn, but on older forests that burn. Clearly, the relationship between pre-fire forest structure and post-fire bird communities deserves more attention.

A comparison of the bird communities in recent clearcuts and recent burns (Fig. 1) reveals a fair amount of similarity in the face of some important differences between the two cover types (Table 3), due primarily to

the presence of standing dead trees in the burned sites, which are used for feeding and/or nesting purposes by a large number of bird species (see also Davis 1976). I found an even greater overall similarity between clearcuts and burns that are in mid-successional stages, suggesting that, when considered over all post-harvest successional stages, clearcutting may come closer to matching the natural patterns of bird occupancy on a patch of land than do many (or most) other cutting practices. I must reiterate, however, that the relative abundances of many species differ quite markedly between recently burned and recently cut forests. Even in mid-successional burns and clearcuts, which showed a greater relative similarity in bird-community composition than the earlier stages did, there were still significant differences in the absolute abundances of a large number of individual species (for example, compare the two abundance estimates for Calliope Hummingbird, Red-naped Sapsucker [*Sphyrapicus nuchalis*], Clark's Nutcracker, and Cedar Waxwing [*Bombycilla cedrorum*]). Therefore, even though the bird communities in clearcuts begin to look similar to those in fire-disturbed forests after a decade or two (Fig. 1), the bird communities are still quite different (in an absolute sense) from those that occur after a natural fire. Perhaps the best alternative to traditional harvesting methods in forests that evolved under standard-replacement fire regime may be to conduct some sort of partial harvest, after which the remaining forest would be burned lethally.

Fire (and its aftermath) should be seen for what it is: a natural process that creates and maintains much of the variety and biological diversity of the Northern Rockies. Most current cutting practices neither create large amounts of standing dead timber nor allow forests to cycle through stages of early succession that are physiologically similar to those that follow stand-replacement fires. Unless managers begin to couple lethal burning with their cutting practices in those forests that evolved under stand-replacement fire regimes, traditional land-management practices will not achieve the goals of ecosystem management.

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Landscape Characteristics of Fragmented Shrubsteppe Habitats and Breeding Passerine Birds

1994

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Abstract: We examined the influence of local and landscape-level attributes of fragmented habitats in shrubsteppe habitats on the breeding distributions of Sage (Amphispiza belli) and Brewer's (Spizella breweri) Sparrows, Sage Thrashers (Oreoscoptes montanus), Horned Larks (Eremophila alpestris), and Western Meadowlarks (Sturnella neglecta) in the Snake River Plains of southwestern Idaho. We developed habitat (resource) selection models for each species by combining bird counts conducted from 1991 through 1993 with local vegetation characteristics and landscape attributes derived from satellite imagery. Site selection by shrubsteppe species (Sage and Brewer's Sparrows, and Sage Thrashers) depended on local vegetation cover and landscape features, such as the patch size of shrub habitats or the spatial similarity of sites. Marginal sites for these species (with species present in one of three years) were intermediate between unoccupied (never present) and occupied sites along environmental gradients characterized by increasing size of shrub habitat patches and total shrub cover and by decreasing disturbance. Horned Larks and Western Meadowlarks, typical grassland species, were not sensitive to landscape features, and their occupancy depended on the amount of grassland or shrub cover. In contrast to shrubsteppe species, sites that varied by occupancy rates of Western Meadowlarks did not significantly differ in vegetation or landscape components. Our results demonstrate that fragmentation of shrubsteppe significantly influenced the presence of shrub-obligate species. Because of restoration difficulties, the disturbance of semiarid shrubsteppe may cause irreversible loss of habitat and significant long-term consequences for the conservation of shrub-obligate birds.

A
marginal =
present
in one
of 3 years

Características del paisaje en ambientes fragmentados de estepas arbustivas y pájaros paserínidos en estado reproductivo

Resumen: Examinamos la influencia de los atributos a nivel local y del paisaje de los hábitats fragmentados dentro de ambientes de estepas arbustivas, sobre las distribuciones reproductivas de los paserínidos Amphispiza belli y Spizella breweri, Oreoscoptes montanus, Eremophila alpestris y Sturnella neglecta en las planicies del Río Snake del Sudoeste de Idaho. Desarrollamos modelos de selección de hábitats (recursos) para cada especie, combinando conteos de pájaros llevados a cabo entre 1991 y 1993 con características de la vegetación local y los atributos del hábitat derivados de imágenes de satélite. La selección de los sitios por parte de las especies de arbustos de las escarpas o pendientes (Amphispiza belli y Spizella breweri) dependió de la cobertura de la vegetación local y las características del paisaje, tales como el tamaño de los parches de los ambientes arbustivos o similitud espacial de los sitios. Los sitios marginales para esas especies (aquellos con las especies presentes en solo 1 de los 3 años) fueron intermedios entre los desocupados (nunca presentes) y los sitios ocupados, a lo largo de gradientes ambientales caracterizados por un incremento en el tamaño de los parches del ambiente arbustivo y la cobertura total de arbustos y un decrecimiento en la perturbación. Eremophila alpestris y Sturnella neglecta, especies típicas de pastizales, no fueron sensibles a las características del paisaje y dependieron de la cantidad de cobertura de pastizal o de arbustos. En forma opuesta a las especies de las estepas arbustivas, los sitios que variaron en cuanto al grado de ocupación de Sturnella neglecta, no presentaron

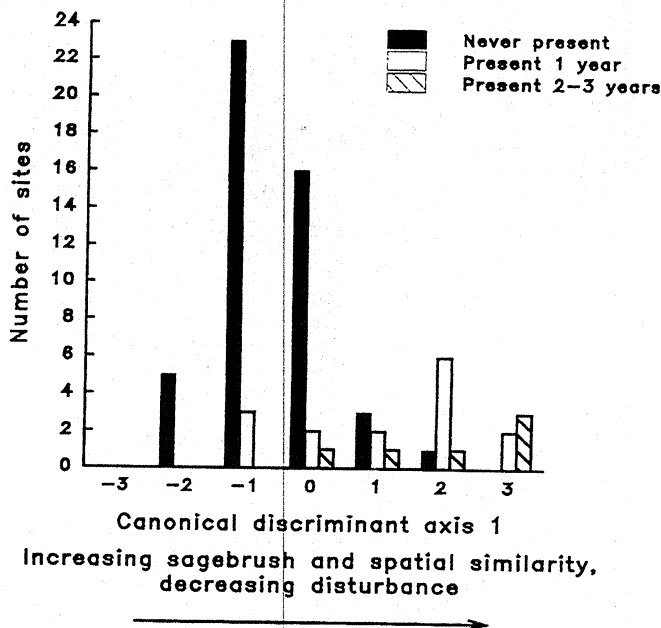


Figure 9. Histogram of canonical scores for sites where Brewer's Sparrows were observed in zero, one, or two to three years at 69 sites surveyed in three consecutive years.

sites for Sage Thrashers were intermediate along the first canonical axis between occupied and unoccupied sites (Fig. 10). Horned Larks were present at all 69 sites in all years. Therefore, we omitted Horned Larks from this analysis.

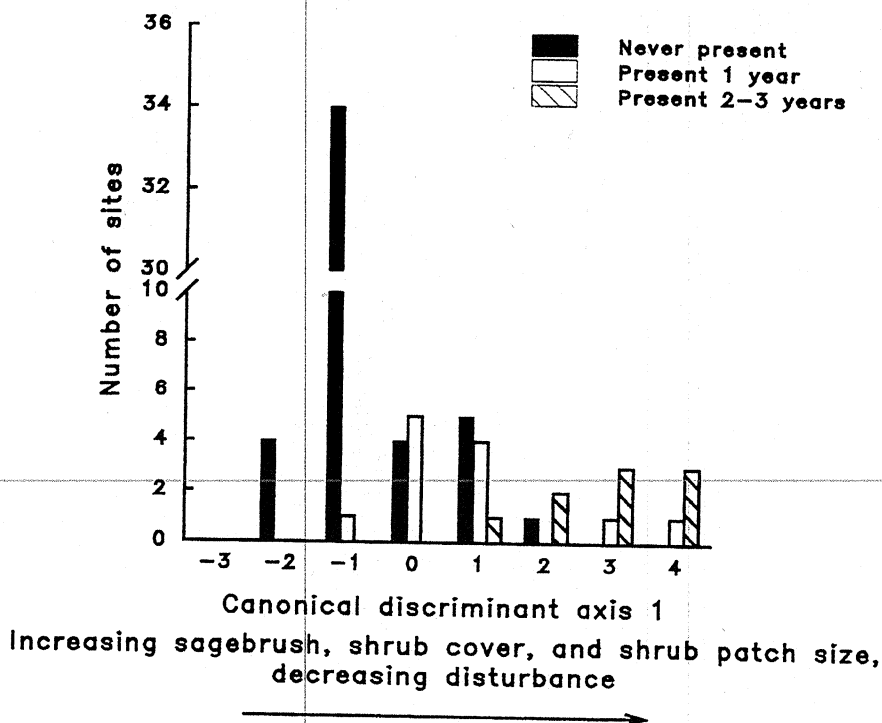


Figure 10. Histogram of canonical scores for sites where Sage Thrashers were observed in zero, one, or two to three years at 69 sites surveyed in three consecutive years.

Western Meadowlarks were observed at 45 sites in two to three years, at 17 sites in one year, and were absent at 7 sites. The MANOVA was not significant in testing the hypothesis that habitat variables were different among occupancy classes (Wilks' Lambda = 0.648; $df = 22, 112$; $p = 0.236$), and separation by occupancy class was not significant (Table 3).

Discussion

The relationship of habitat fragmentation to pattern of avian distribution in forested landscapes has been well documented (for example, Robbins et al. 1989). Although others have examined fragmentation in shrublands (Soulé et al. 1988; Bolger et al. 1991) or the relative contributions of local and landscape features (Bergin 1992; Pearson 1993), we believe our study represents the first to demonstrate the importance of combining these attributes.

Our habitat-selection models were consistent with previous local-scale habitat associations described for Sage and Brewer's Sparrows and Sage Thrashers. For these species, total shrub cover and abundance of shrub species—predominantly sagebrush—are important habitat characteristics (Rotenberry & Wiens 1980a, 1980b; Wiens & Rotenberry 1981; Rotenberry 1986; McAdoo et al. 1989). Moreover, our study also emphasized the additional importance of landscape characteristics for these shrubsteppe species, especially those relating to fragmentation (Table 2). In contrast, Horned Larks and

Western Meadowlarks, typical grassland species, were insensitive to the landscape features at our scale of measurements and were influenced primarily by grasslands or lack of extensive shrub cover. This also is consistent with previous observation of these species in shrubsteppe habitats (Wiens & Rotenberry 1981), although fragmentation of grasslands has influenced the presence of Horned Larks and Western Meadowlarks in other regions (Johnson & Temple 1986, 1990; Samson 1980). In our study, Western Meadowlarks were associated with areas dominated by grasslands containing a sparse cover of emergent shrubs (Fig. 6), which were used as song perches. The ubiquity of Horned Larks suggests that the scale of our sampling may be fairly coarse or that, at a larger regional scale, even the most shrub-dominated areas were fragmented.

Habitat-selection models were not statistically evaluated with any interaction terms. But it is clear that, for Sage Sparrows and Sage Thrashers, landscape features interact with local habitat variables to alter the expression of probability of occupancy (Figs. 3 & 5). For example, the form of the relationship between percentage sagebrush cover and probability of occupancy of Sage Sparrows depicted in Fig. 3, although always positive, changed shape as a function of shrub patch size (compare the front right edge of the surface in Fig. 3 to the back left edge). Thus, differences in the structure of landscapes in which local study plots are embedded may produce differences in apparent bird-habitat relationships derived from those local plots (Wiens & Rotenberry 1981; Collins 1983; Petersen & Best 1987).

Abundances of migratory shrubsteppe bird populations characteristically are highly variable across time and space (Rotenberry & Wiens 1980b; Wiens & Rotenberry 1981). Much of this variation has been attributed to events away from the breeding grounds during the nonbreeding season (Rotenberry & Wiens 1980b; Wiens & Rotenberry 1981). In this study we demonstrated that local habitat attributes, combined with landscape features on the breeding grounds, also were associated with the temporal persistence of populations. All three typical shrubsteppe species were more likely to return to sites that had high shrub cover (particularly sagebrush) and low disturbance, combined with large patch sizes and high within-site spatial similarity (Table 3). Although disturbance (as indicated by percentage cover of Russian thistle) was not significant in any of the habitat selection models, it was significant in the canonical analyses for all these species. Thus, habitat disturbance and fragmentation were associated not only with the probability of occurrence of a species among sites within years but also between years.

Fragmentation of shrubsteppe habitats by wildfire (Whisenant 1990), shrub die-off (Pyke & Dobrowolski 1989), or human-caused disturbance (Braun et al. 1976) appears to significantly affect obligate species, such as

Sage and Brewer's Sparrows and Sage Thrashers. Prior to the mid-1800s, the Snake River Plain and northern Great Basin, particularly southwestern Idaho, were dominated by sagebrush and saltbush shrubsteppe interspersed with patches of native bunchgrasses in recently burned areas. These shrub-dominated mosaics often covered hundreds of thousands of contiguous hectares (Frémont 1845; Yensen 1980; Young 1989). Thus, these bird species likely were adapted to a landscape dominated by vast tracts of shrublands and have been exposed to an ecosystem whose structure and function has been altered by fragmentation only recently in ecological time. That Horned Larks and Western Meadowlarks appear less affected by landscape features may be because they are at the margin of their ecological distribution along a continent-wide grassland-shrubland gradient (Wiens & Rotenberry 1981).

We do not know the specific mechanisms by which fragmentation influences shrubsteppe species, although the scale at which species presence was influenced was much larger than the size of individual home ranges, similar to the effects of fragmentation in forested regions (Robbins et al. 1989; Freemark & Collins 1992). Species' characteristic dispersal and reproductive rates, specialization, and dependence on the fragmented resources (Urban & Shugart 1984; Fahrig & Paloheimo 1988), coupled with patch size and interpatch distance (connectivity) of the habitats (Gardner et al. 1987; Burkey 1989) dictate benefits or loss due to habitat fragmentation. Birds in fragmented habitats have exhibited both lower reproductive and higher predation rates (Wilcove 1985; Yahner & Scott 1988; Robinson 1992; Perneluzi et al. 1993) and either or both may operate here.

Fragmentation of shrubsteppe habitats is of concern for the conservation of obligate species. The rapid loss of resident bird species in another fragmented shrubland ecosystem, southern California chaparral, has already been documented (Soulé et al. 1988; Bolger et al. 1991). Unlike in forested regions (Harris 1984), the impact of fragmentation on obligate species in the Snake River Plain and Great Basin shrubsteppe may be more permanent. Conversion of shrubsteppe into annual grasslands is accelerated because disturbance promotes the establishment of exotic annuals and increases the frequency of fire. This positive feedback creates habitat sinks from which recovery via natural plant-successional processes is unlikely (Young & Evans 1978; West 1979; Allen 1988). Without large-scale active restoration (Allen & Jackson 1992; Milton et al. 1994), this ecosystem and its obligate species are at risk (Young et al. 1979).

Acknowledgments

We thank P. Bates, D. Johnson, and K. Kesling for field assistance. Funding was provided by the U.S. Bureau of

The Salt Lake Tribune

The juniper mystery: Why is a tree that's supposed to withstand drought suddenly dying in southern Utah?



(Courtesy photo | Kate Magargal, University of Utah) Scientists and federal land managers are scrambling to investigate widespread juniper mortality in southeast Utah. Researchers shot this photo last month on Cedar Mesa, where junipers started dying in droves in September after the driest and warmest year on record. Foresters are stumped because juniper is seen as a drought-tolerant species.



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By Brian Maffly • Updated: November 20, 2018

The Utah juniper is considered the West's most drought-tolerant and resilient conifer, withstanding even the worst dry spells while nearby pinyon and ponderosa drop their needles and die.

So it was with some alarm for Kay Shumway, a retired science educator from Blanding, when he noticed yellowing among the juniper on southeastern Utah's Moki Dugway last spring, a time of year when these trees' needles should carry a vivid shade of green as they ramp up their photosynthetic capacity.

"During summer, the dying junipers were such a bright yellow color. It was easy to see. You could look out over the landscape and see thousands of those dying trees. Now a lot have dropped their needles and are becoming a skeleton," said Shumway, a former botanist who has kept himself busy as a nature photographer since retiring from the College of Eastern Utah 20 years ago. "They are dying. They are not going to come back [even if they get] some moisture."

He frequents the Moki Dugway on the southern tip of Cedar Mesa, which provides photogenic views of the buttes and canyons falling toward the San Juan River in what was initially part of Bears Ears National Monument.

Shumway has since documented dying juniper in other parts of San Juan County, which is in the midst of a severe drought.

"My first reaction was the drought was causing it. The interesting thing is the pine trees, which are the most susceptible to drought, aren't affected. They are still green and healthy," Shumway said. "There were more and more of [the juniper] turning yellow. By July, I went all over the county, like Mustang Mesa and Alkali Ridge [east of Blanding]. Lo and behold, it was happening there, too."

Shumway has shared his photos and drone footage with academic scientists and forestry officials, who are now scrambling to determine the extent and causes of Utah's latest round of tree mortality.

The Colorado Plateau just experienced its driest year on record. Bluff saw barely 2 inches of precipitation in the water year that ended Sept. 30, about a fourth of normal, according to a National Weather Service database.

But juniper should be able handle a dry year.

"You can't look at the weather data for one year. Often the stress from drought is lagged," said entomologist Liz Hebertson. "We would have to look at conditions back three years, six years, 10 years. When a tipping point occurs might be different between species and even individual trees."

Other factors, working in combination with climate change, are probably at play, according to Hebertson, who works with the U.S. Forest Service's Forest Health Protection program in Ogden.

"It could be the perfect storm of other factors," Hebertson said. "Right now, we have a lot of questions."

Like what is the extent of the mortality? What are the elevation profiles, soil conditions and other environmental characteristics of the affected areas? Are there signs of beetle infestation? Is the wood discolored? Are other tree species showing signs of distress?

Utah is no stranger to conifer die-offs. Dixie National Forest outside Cedar City is ground zero in a beetle epidemic that wiped out spruce, while lodgepole pines are falling victim to beetles in the Uinta Mountains. Ghost forests stretch across basins and plateaus for miles around the West.

Hebertson and her colleagues have been preoccupied this year with a new infestation afflicting forests in northern Utah, where a nonnative beetle, the balsam woolly adelgid, is decimating subalpine fir. This tree mortality is just as troubling as the one unfolding in San Juan County.

In search of clues in the juniper deaths, Hebertson is leading numerous scientists on a tour near Blanding later this month, along with Shumway, who wishes the group came earlier while the yellowed foliage was still hanging from the juniper branches.

"I'm thrilled to know there is some work being done on it," Shumway said. "I'm going to have this group get up close and personal with these trees, though it won't be as easy to see. You can still see there are dying trees all over the place."

Since retiring from CEU (now part of Utah State University), where he served as dean of instruction after helping to establish the Blanding campus in 1977, Shumway has explored Bears Ears country with cameras in tow. While stressed junipers have been documented across the state line in Colorado since last year, Shumway was the first to systematically record the phenomenon in Utah.

Almost more a shrub than a tree, Utah junipers crowd valley bottoms and mesa tops all over the Beehive State. They often mistakenly were called cedars in pioneer times; hence the appearance of the word "cedar" in so many Utah place names.

Junipers, along with the pinyons they usually grow with, are the subject of vegetation-removal operations in the name of habitat improvement. But these trees play a vital ecological role, stitching landscapes together and providing habitat for countless animals.

Widespread loss of junipers would have far-reaching consequences for southern Utah's fragile desert environments. Among those taking a keen interest is University of Utah biology professor Bill Anderegg, who studies the impact of climate change on forest ecosystems.

"What we see is worrying and it's mind-boggling because juniper has weathered drought. In the drought of 2002, they were not affected," Anderegg said. "To see juniper die on a landscape scale is pretty disturbing. The pinyon don't seem to be dying at the same rate."

A possible factor is the Western cedar borer or cedar bark beetle, insects known to attack juniper. Shumway has pulled bark off dead trees to find larvae munching on the phloem, the critical tree tissues that conduct the fruits of photosynthesis to the root system.

But the presence of beetle larvae is just a clue, not a complete causal picture.

Last year was not only the driest on record for Utah, but it also was the second warmest. Could warm weather be compromising the trees' health, undermining their ability to repel beetle attacks? Or could it be enabling populations of hungry beetles to explode?

"We want to know how bad is the mortality event, how prevalent it is across the Four Corners, pin down the drivers," Anderegg said. "What are the thresholds that push junipers over the edge, and why are those thresholds being crossed now?"

Anderegg has applied for a Forest Service grant to explore such questions. At this stage, however, the extent of juniper mortality has yet to be established, much less why it might be happening, although few doubt climate change is playing some role.



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Montana Partners 'Flight

Montana Bird Conservation Plan
Version 1.0 - Jan. 2000

workshops, ecologically sensitive area of remnant grassland and shrubsteppe in the northern Great Plains (The Nature Conservancy 1999). We will build upon this effort to implement conservation measures in these polygons.

Land Trusts. Land trusts are non-profit organizations that help landowners find ways to protect their land in the face of ever-growing development pressure. They work with landowners to write conservation easements (permanent deed restrictions that prevent harmful land uses), acquire land through donation and purchase, or devise other plans to maintain all kinds of open space—wetlands, wildlife habitat, ranches, shorelines, forests, scenic views, farms, watersheds, historic estates, and recreational areas. There are at least 10 land trusts operating on a statewide, regional or local level in Montana (Appendix C), including the Montana Land Reliance, Trust for Public Lands, Five Valleys Land Trust, the Nature Conservancy, and the Rocky Mountain Elk Foundation. Well over 600,000 acres have been protected through conservation easements in Montana, the highest state total in the United States (Montana Fish, Wildlife and Parks 1999).

THE PRIORITIZATION PROCESS

Species Prioritization

Partners in Flight uses a system that identifies species of conservation priority in each of its planning units, rather than writing planning information about all species. It is assumed that if conservation measures are focused on these species and their habitats, the other species in the area will benefit as well.

We identified a pool of species from among the breeding avifauna, which represents priorities for conservation action within Montana (Table 2). Note that a species may be considered a priority for several different reasons, including global threats to the species, high concern for regional or local populations, or high state responsibility for conserving large or important populations of the species. The different potential reasons for priority status are represented by shaded cells in Table 2. Our primary means of prioritizing species was through the PIF prioritization scores generated by the Colorado Bird Observatory (Hunter et al. 1993, Carter et al. 1998). This system ranks species according to seven measures of conservation vulnerability. These include four global measures (i.e., they do not change from area to area), as well as measures which are specific to each physiographic area or state. A total rank score is then derived, which is a measure of overall conservation priority; scores for all breeding species in Montana are found in Appendix B.

The Partners in Flight Species Prioritization scheme was first developed in 1991, and has been continually reviewed and refined in the years following inception (Carter et al. 1998). The system ranks each species of North American breeding bird based upon seven measures of conservation "vulnerability". These factors include relative abundance (interspecific; RA), size of breeding (BD) and non-breeding (ND) ranges, threats to the species in breeding (TB) and non-breeding (TN) areas, population trend (PT), and relative density (intraspecific; AI) in a given planning unit compared to the maximum reached within its range. Each species is given a score of 1-5 in each category, with 1 indicating the least amount of vulnerability with regard to that parameter and 5 the most. Scores in each category are then summed to produce a composite score potentially ranging from 7-35. Species with relatively high overall scores (e.g. >22) are considered most vulnerable to extinction (although they often are not endangered at present) and usually need conservation measures or at least need to be carefully monitored through their ranges.

We used the following criteria to help us select priority bird species in Montana:

Rockies. Its nomadic nature makes it hard to monitor and to manage for. Habitat manipulations that influence cone production have implications for the species' productivity. Montana has potential as an excellent area to investigate the relationships between crossbill races, tree species forest management.

Distribution. The Red Crossbill is distributed throughout the west from eastern New Mexico north to Alaska then east across southern Canada (north of the Great Plains region) and northern United States. Breeding has been documented throughout most of Montana with the exception of the northeast corner (Montana Bird Distribution Committee 1996).

Habitat Requirements. The Red Crossbill is found within a wide variety of mature coniferous forests and mixed deciduous/coniferous forest. Usually they are associated with mature open canopy tree stands. They have been found in types ranging from dry savannah ponderosa pine, Douglas-fir, up to grand fir and subalpine fir types. Gap analysis (Redmond et al. 1998) identified 6.5 million ha of Crossbill habitat in the State.

Ecology. The Red Crossbill is a very nomadic species with its distribution and reproduction tied to the coniferous seed crop production. Breeding can occur at almost any time of the year. Research has indicated that there are up to 6 distinct forms of Red Crossbills, which differ in song type and in morphology. Though little is known of the individual distribution of these types in the state, each is apparently adapted to feed on the cones of a different tree species. Several of these (potential species) do occur in Montana.

Management Recommendations. Any silvicultural treatments which emphasize seed production in conifers are likely to improve habitat suitability for this species. In Dry Forest, maintaining some element of Douglas-fir is important for those crossbills adapted to feed on its smaller seeds, in addition to those adapted to feeding on ponderosa pine. Douglas-fir is also most likely the preferred tree for nesting.

DF

Habitat and Population Objectives: Dry Forest

Mature Ponderosa Pine Restoration. Restoration activities in dry forest habitat types are important due to the dramatic changes in tree species composition and stand structure that have affected most dry forest habitat in western North America. An awareness and understanding of these changes, and the desirability of restorative activities in ponderosa pine habitat, is ubiquitous in Forest Service regions in the American West. The political will (or feasibility) and financial resources to accomplish restoration, however, vary throughout the West (Amundson 1998; Denton 1998; Dick 1998; Shafer 1998)

Habitat Objectives for Dry Forest

- Retain all current old-growth stands that meet minimum regional old-growth characteristics (Table 8). Restore historic structural characteristics with no elimination of large trees or snags.
- Manage for the long-term maintenance of 25% of dry forest habitat (per 4th order watershed) as old growth based on mean values of regional old-growth characteristics (Table 9). Values for old-growth characteristics should be no lower than 25% below mean values; and 50% of old-growth stands should meet or exceed regional mean values for old-growth elements.

25%

Table 8. Minimum values of old-growth characteristics, Dry forest habitats (ponderosa pine and Douglas-fir), USFS Region 1 (Green et al. 1992)

<u>Forest Types</u>	<u>Ave. Age of Large Trees</u>	<u># Large Trees</u>
Warm, dry ponderosa pine (west side)	170 yr	8 trees/ac $\geq$ 21 in dbh
Cool, dry Douglas-fir (west side)	170 yr	8 trees/ac $\geq$ 21 in dbh
Warm, dry ponderosa pine (east side)	180 yr	4 trees/ac $\geq$ 17 in dbh
Cool, dry Douglas-fir (east side)	200 yr	5 trees/ac $\geq$ 19 in dbh

- Restore the role of fire, and use thinning as necessary, to restore historic conditions.
- Retain all snags and broken-top trees $\geq$ 9 in dbh and all large trees $\geq$ 17 in dbh in harvest units.
- Manage for single- and double-storied stands with open conditions (<50% cover) in dry forest habitat of all age classes.

Table 9. Mean values of old-growth characteristics, Dry forest habitats (ponderosa pine and Douglas-fir), USFS Region 1 (Green et al. 1992)

<u>Forest Type</u>	<u>Ave. Age of Large Trees</u>	<u># of Large Trees</u>	<u># Standing Dead Trees</u>
Warm, dry ponderosa pine (west side)	246 yr	17 trees/ac $\geq$ 21 in dbh	6 trees/ac $\geq$ 9 in dbh
Cool, dry Douglas-fir (west side)	232 yr	18 trees/ac $\geq$ 21 in dbh	7 trees/ac $\geq$ 9 in dbh
Warm, dry ponderosa pine (east side)	215 yr	24 trees/ac $\geq$ 17 in dbh	7 trees/ac $\geq$ 9 in dbh
Cool, dry Douglas-fir (east side)	229 yr	31 trees/ac $\geq$ 17 in dbh	10 trees/ac $\geq$ 9 in dbh

- Manage for a variety of habitat conditions at the landscape level, particularly varied understory conditions, to meet the needs of the Flammulated Owl and Lewis's Woodpecker.

Priority Species Objectives.

The absence of suitable nest sites is usually considered the limiting factor for cavity-nesting species (Thomas et al. 1975). Retention of all existing large snags and broken-top trees, and management for adequate numbers over the landscape is a critical objective in order to maintain viable populations of Lewis's Woodpeckers and Flammulated Owls. The retention of all snags and broken-top trees $\geq$ 9 in. dbh and all

habitat.

Distribution. The Townsend's Warbler breeds from southeastern Alaska, south through western Canada to central and northeastern Oregon, northern Idaho, northwestern and southcentral Montana, and northwestern Wyoming. In Montana, it only breeds in the western quarter of the state (Montana Bird Distribution Committee (1996). It winters in central and southern California, western Mexico, and the highlands of Central America.

Habitat Requirements. Townsend's Warblers nest in coniferous forests or mixed coniferous/deciduous forests where coniferous trees comprise a predominant feature of the habitat (Bent 1953, Erskine 1977). Surveys in northern Idaho and Montana detected them most frequently in cedar-hemlock forests, followed in order by mixed conifer, spruce-fir, Douglas fir, riparian shrub (probably adjacent or within forest), lodgepole pine, and ponderosa pine (Hutto 1995). In those surveys, they were less abundant in drier and more open forest cover types and in forest patches that have been harvested. They were more likely to occur on points with a few or lots of snags within 10 m (30 ft) of the survey points and were nearly 5 times more common on points with a lot of dead and down material (Hutto 1995). In a review of several studies, Hejl et al. (1995) listed the Townsend's Warbler as an old-growth associate in studies in Montana, Idaho, and Oregon, although another Idaho study found them present but not clearly associated with old-growth, mature, or immature forests. Hejl et al. (1995) found Townsend's Warblers to be less abundant in clearcut or partially cut forest than in uncut forest.

Ecology. Townsend's Warblers build cup-shaped nests in and near the tops of coniferous trees on a branch well away from the trunk. They feed mostly on insects (e.g., weevils, bugs, leafhoppers, caterpillars) and spiders, gleaning them from the foliage or hawking them from the air (Ehrlich et al. 1988, Groves et al. 1997). Herman and Bulger (1979) found breeding densities of 10-47 pairs/40 ha (100 ac) in Oregon mixed-coniferous forests.

Management Issues. Hutto (1995) stated that the Townsend's Warbler is probably one of the more sensitive species to timber harvesting activity as evidenced by a continuous decline in probability of occurrence with increasing amounts of timber removed. It appears from Hutto's data that they are found more frequently on points where no edge is within 100 m (305 ft). Management at the landscape level should allow for retention and recruitment of mature mixed conifer stands.

Habitat and Population Objectives: Moist Douglas-fir and Grand fir

Habitat Objectives - Old Growth:

- Existing old-growth stands (> 170 years, meeting minimum criteria for region and forest type: Green) should be retained whenever possible, especially in areas that are in likely refugia from stand-replacement fires.
- Maintain mature or overmature stands for recruitment into old growth, toward goal of 20% of the

20%

habitat type managed for old-growth conditions; these should be located in likely refugia from fire or in areas providing connectivity to isolated old-growth stands.

- Abnormally dense young to mature stands surrounding old growth could be targets for forest health treatment (thin-from-below or partial cut) to reduce the risk of fire spread into old-growth stands.
- Old-growth should be well-scattered throughout forest lands rather than grouped into adjacent areas (McClelland et al. 1979); stands may be of variable size but most should be at least 50-100 acres (McClelland et al. 1979), imbedded within an area of 364-1000 acres of mature or partial cut forest managed snag and log retention (McClelland et al. 1979, Bull and Holthausen 1993). Some larger blocks, especially in mesic areas where historically more likely (see Pileated Woodpecker).
- Encourage retention of snags and logs in all silvicultural treatments [Bull and Holthausen recommended > 8 snags/ha, at least 20% of which are > 50 cm, and . 100 logs/ha, with a preference for logs > 38 cm]
- Refrain from sanitation cutting of insect-killed trees within the 20% of lands managed for old-growth; limit firewood cutting to snags less than 40 cm and discourage use of larch, ponderosa pine, and broadleaf species (McClelland et al. 1979).

Prescribed Fire: (see also section on Burned Forests)

- Expand the opportunity for allowing lightning fires to burn.
- Re-ignite suppressed lightning fires when conditions come back into prescription.
- Use broadcast burning to restore normal fuel conditions so that lightning fires can be allowed to burn.
- Capitalize on opportunities to develop stand conditions that approximate those created by stand-replacement fire regimes.

Timber Harvest:

- Vary timber harvest methods, using more even-age prescriptions ("messy" clearcuts and seed-tree cuts) in more mesic sites that would have historically had stand-replacement fire regimes. Retain seed trees permanently, preferably large larch (> 40 cm), and retain snags and occasional clumps of green trees.
- Produce a diversity of stand structures in mixed and variable fire regime types. Some regular thinning methods may be appropriate, but vary with more heterogeneous stand prescriptions. Leave clumps of intact forest, snags, and large logs.

State of the Birds Report

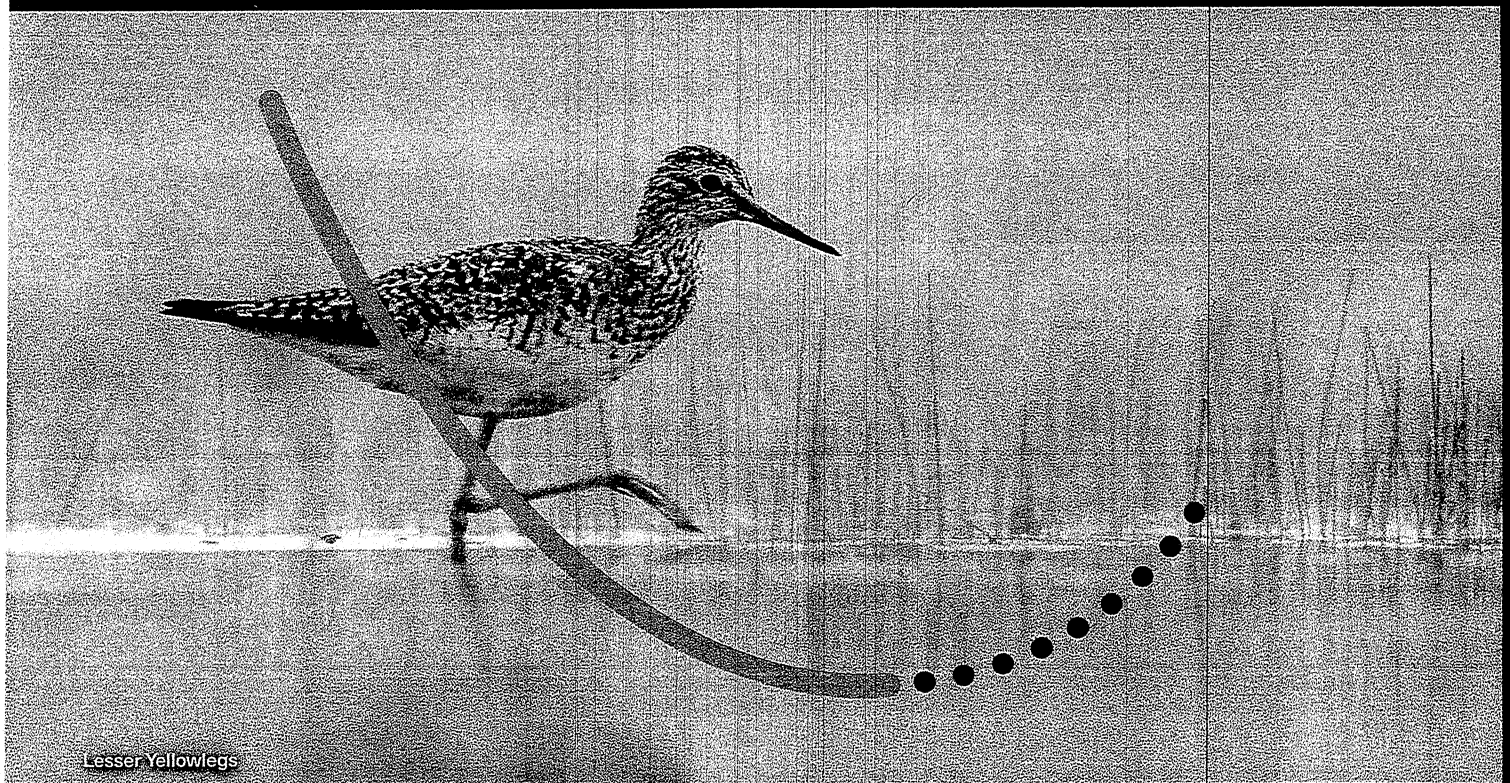
United States of America

2022



We Can Bend the Curve to Bring Birds Back

The United States and Canada have lost 3 billion breeding birds since 1970—a loss of 1 in 4 birds, according to research published in *Science* in 2019. This steep decline in abundance can be reversed with new scales of conservation actions that benefit not only birds but also wildlife and people.



Lesser Yellowlegs

When Birds Thrive, We All Win

State of the Birds at a Glance

The trends for our nation's birds reveal a vital message. Birds are declining overall in every habitat except in wetlands, where decades of investment have resulted in dramatic gains.

Conservation works when we give birds and nature a chance. Let's do more to save our nation's birds and benefit people in every state.

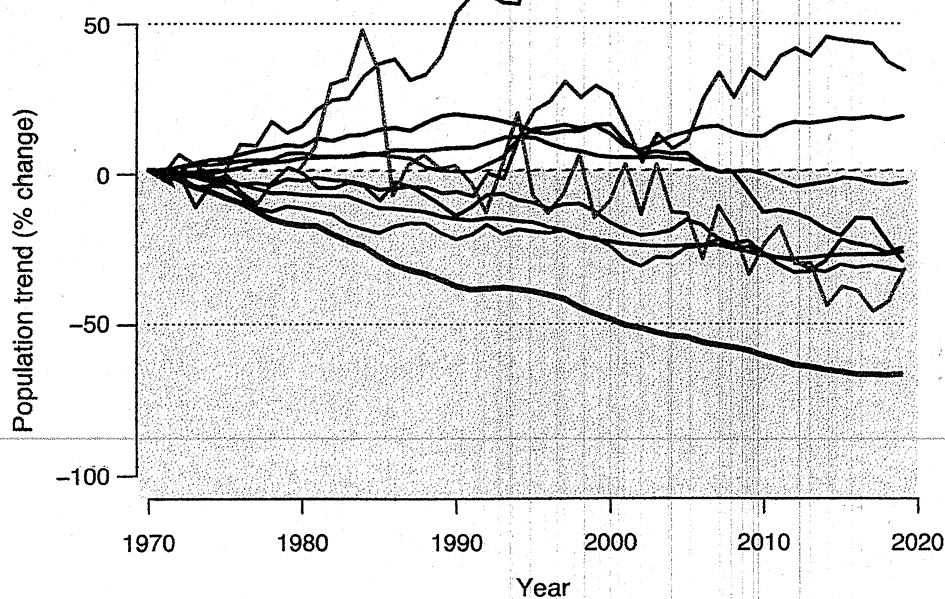
Three billion birds lost

1 in 4 breeding birds have been lost from the United States and Canada in the past 50 years.

70 Tipping Point bird species in the United States

These 70 species have lost two-thirds of their populations in the past 50 years, and are on track to lose another 50% in the next 50 years.

Birds across the U.S. show downward trends in every habitat except in wetlands, where comebacks of waterfowl show the power of funding and policy investments.



+1,076% Geese and Swans

+34% Dabbling/Diving Ducks

+18% Waterbirds

-5% Western Forest Birds

-26% Aridland Birds

-27% Eastern Forest Birds

-30% Sea Ducks

-33% Shorebirds

-34% Grassland Birds

-67% Tipping Point Species

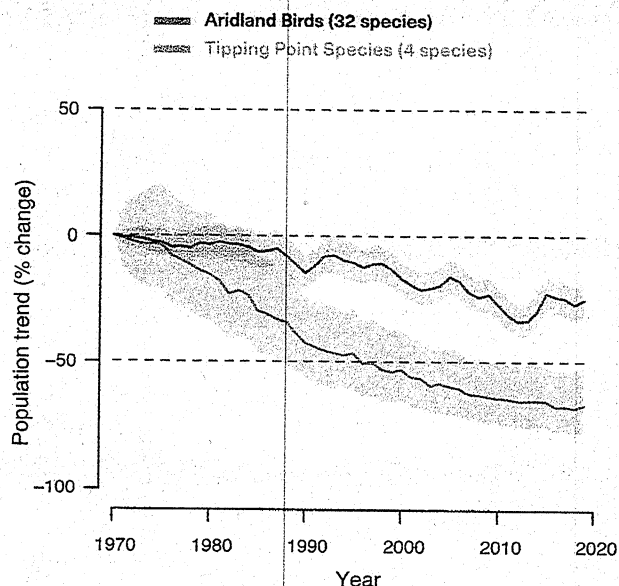
Trends for breeding bird species by group or by habitat during 1970-2019, except for the shorebirds trend, which begins in 1980. For details, see pages 6-13.



Greater Sage-Grouse

ARIDLAND BIRDS A Key Role for Public Lands

Status: Long-term declines with unrelenting habitat threats

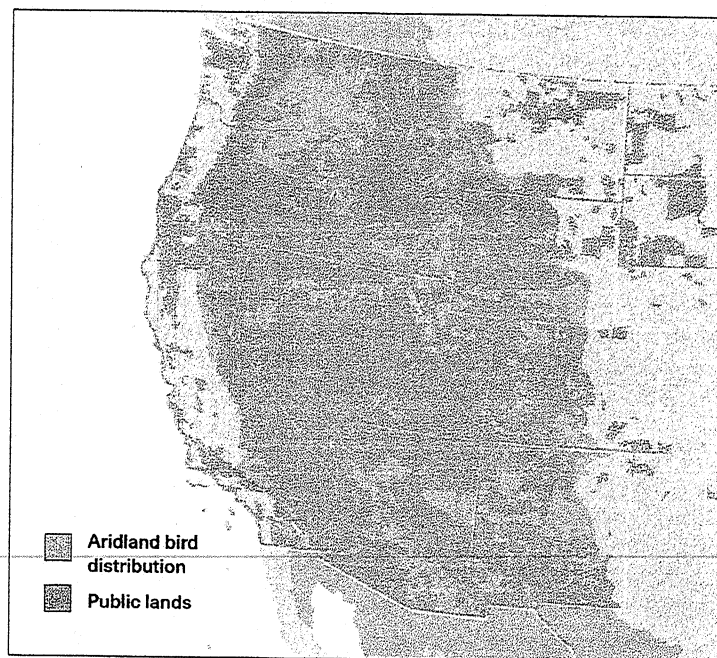


Aridland birds have been in a long-term decline, with a slight improvement since 2012. Fires, drought, invasive plants, development, unsustainable grazing, and energy extraction pressures on habitat are all driving aridland bird declines.

- Several aridland birds (such as Chihuahuan Raven, Sage Thrasher, and Pyrrhuloxia) exhibit accelerated rates of decline since 2010.
- Bendire's and LeConte's Thrasher have experienced long-term declines, but the Bendire's Thrasher population has stabilized in the past decade.
- Greater Sage-Grouse shows a continued steep decline that warrants increased voluntary habitat conservation incentives and renewed strong federal and state protections.

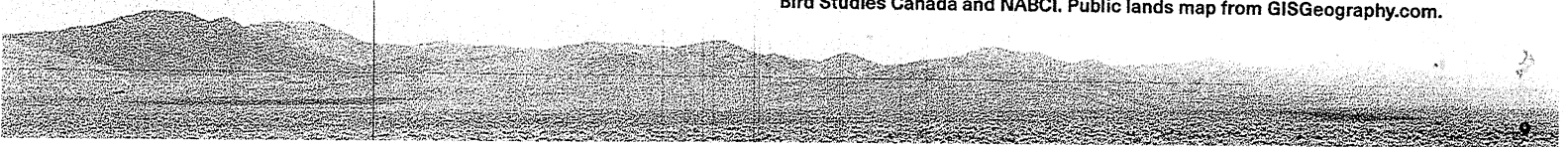
Public Lands Are Essential for Aridland Bird Conservation

The federal government and state agencies have a vital role to play in turning around bird declines in sagebrush and desert habitats. According to the 2011 State of the Birds report, public lands in the American West support more than half of the breeding distribution of aridland birds. Bureau of Land Management lands are particularly important, supporting almost a quarter of the distribution of all aridland birds and more than two-thirds of the U.S. distributions of Sage Thrasher and Sagebrush Sparrow, both species with declining populations. U.S. Forest Service lands in coastal chaparral habitats are important for the declining Wrentit. National Park Service lands are important for some desert bird species, such as the Bendire's Thrasher (a Tipping Point species). The 2011 State of the Birds Report found that about 80% of publicly owned aridlands were vulnerable to activities that could potentially degrade bird habitat—including energy development, off-road vehicle traffic, grazing, mining, and logging. Aridland bird habitat conservation can be compatible with multiple land uses, but management plans for these landscapes need to include measures to ensure long-term healthy populations of aridland birds.



WESTERN PUBLIC LANDS ARE HABITAT FOR ARIDLAND BIRDS

This map shows the cumulative range for 30 aridland bird species in North America, with the vast majority of that range falling within the boundaries of federal and state public lands. Source: Aridland bird data from Bird Conservation Regions, Bird Studies Canada and NABCI. Public lands map from GISGeography.com.





Bullock's Oriole

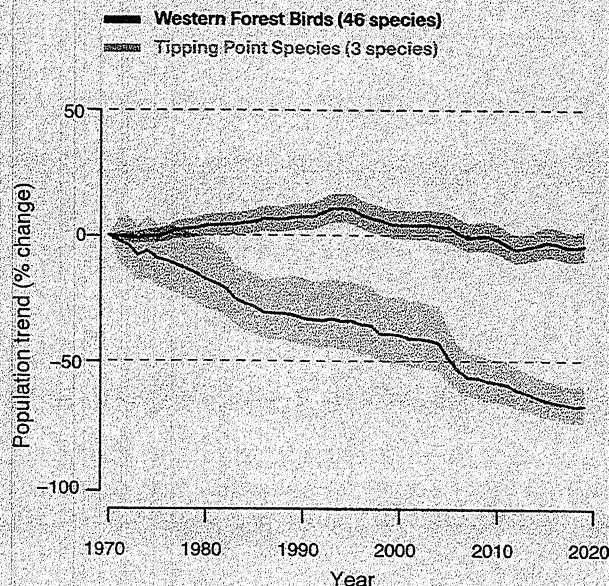
WESTERN FOREST BIRDS

Restoring Natural Cycles for Forest Health

STATUS: Stable overall, but with warning signs

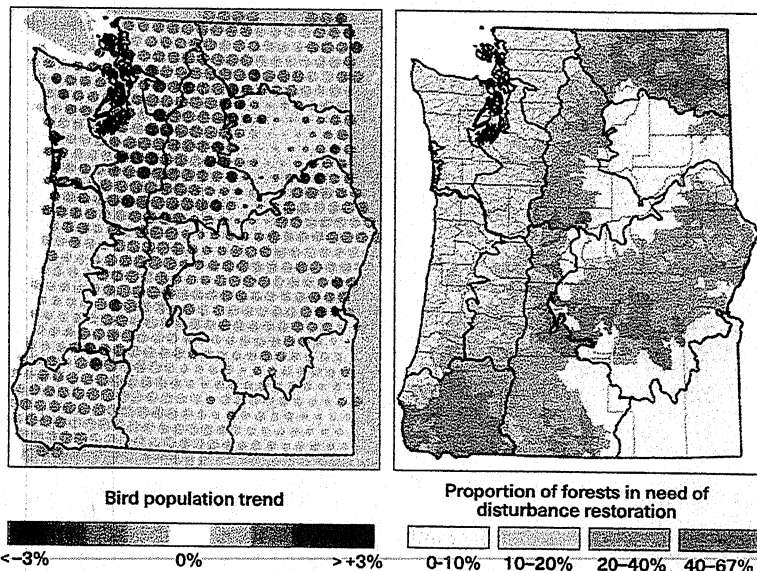
The overall population for the western forest birds group is much the same as it was 50 years ago, aided by protected habitats. But since reaching recent highs in the early 1990s, western forest birds have declined by nearly 20%.

- Almost half of this group (19 species) currently have declining population trends.
- Five species have lost more than half of their population since 1970, including Tipping Point species such as Pinyon Jay and Rufous Hummingbird with poorly understood life cycles. More science is needed to identify the drivers of their declines.
- Recent declining trends among Oak Titmouse, Williamson's Sapsucker, and other birds appear to be associated with the disruption of natural disturbance patterns such as fire cycles.



Birds Are Declining Where Western Forests Are Stressed

For most of the past 100 years, western forests have been managed to encourage conifer tree dominance and discourage fires. But for many centuries before the 1900s, fires were common on this landscape, both natural wildfires and intentional burns by Indigenous peoples. Today those historic disturbance patterns that created a mosaic of conifer and broadleaf forest cover and successional stages have been disrupted, and large swaths of western forest landscapes have departed from their natural range of tree species and structural diversity. These areas of forest departure from natural patterns are also hotspots for western forest bird declines. Furthermore, these compromised forests have very little resilience to the forces of wildfire and climate change, which puts greater forest landscape health and forest resources (such as water reservoirs) at risk of disaster. Investments in forest restoration can turn around this dim outlook for western forests and western forest birds.



BIRD DECLINES IN FORESTS THAT HAVE DEPARTED FROM HISTORIC CYCLES

According to population trends generated by eBird data, bird numbers tend to be declining in forests that have departed from historic conditions and are most in need of disturbance restoration. Sources: Cornell Lab | eBird data 2007-2019 (left map); DeMeo et al, "Expanding Our Understanding of Forest Structural Restoration Needs in the Pacific Northwest," *Northwest Science*, Winter 2018 (right map).

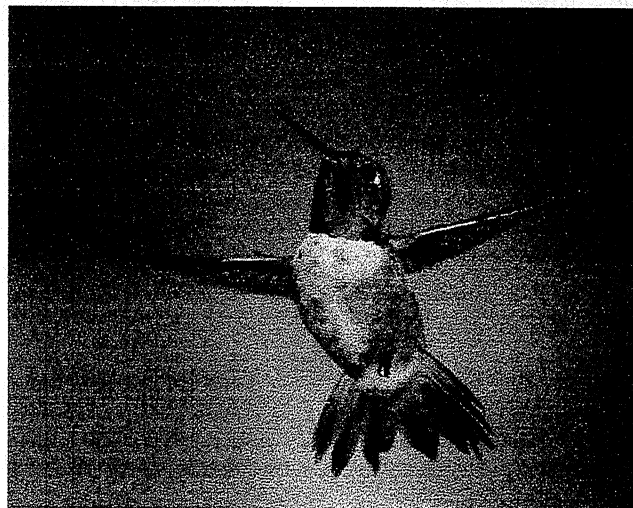
Bird Declines Are Reaching a Tipping Point

Sounding an Alarm About Steep Population Losses

In 2019, a study of 529 bird species with adequate long-term data for analysis (*Science*, Rosenberg et al.) found that 303 species in North America were declining—more than half of the bird species studied.

Now scientists with the Road to Recovery initiative have issued an alert for 90 declining bird species—birds that are not yet federally listed as threatened or endangered, but that have lost half or more of their breeding population since 1970. The scientists further identified a subset of 70 Tipping Point species that could lose another half or more of their populations in the next 50 years, based on recent trajectories and expert assessments.

These Tipping Point species are high priorities for science and conservation because of their high vulnerability to extinction, high urgency, and steep population declines where known. All are included on the Birds of Conservation Concern List of the U.S. Fish and Wildlife Service and/or state lists of Species of Greatest Conservation Need.



Two-thirds of Rufous Hummingbirds have been lost in the past 50 years.

On Alert: All of these bird species have lost half of their populations in the past 50 years

Baird's Sparrow	Allen's Hummingbird	Buff-breasted Sandpiper	King Rail	Rufous Hummingbird ✓
Black-billed Cuckoo	American Golden-Plover	Cassia Crossbill*	Kittlitz's Murrelet*	Saltmarsh Sparrow*
Black Skimmer	Ashy Storm-Petrel*	Chestnut-collared Longspur	Laysan Albatross*	Scripps's Murrelet*
Black Swift	Audubon's Shearwater*	Chimney Swift	Least Tern	Seaside Sparrow*
Canada Warbler	Bachman's Sparrow	Craveri's Murrelet*	LeConte's Sparrow	Semipalmated Sandpiper
Cerulean Warbler	Band-rumped Storm-Petrel*	Elegant Tern*	LeConte's Thrasher	Short-billed Dowitcher
Clark's Grebe	Bendire's Thrasher	Evening Grosbeak ✓	Lesser Prairie-Chicken*	Sprague's Pipit
Eastern Whip-poor-will	Bicknell's Thrush*	Fea's Petrel*	Lesser Yellowlegs	Stilt Sandpiper
Grace's Warbler	Black-capped Petrel*	Golden-winged Warbler	Mottled Duck	Townsend's Storm-Petrel*
Long-billed Dowitcher	Black-chinned Sparrow	Great Black-backed Gull	Mountain Plover	Tricolored Blackbird*
Mourning Warbler	Black-footed Albatross*	Greater Sage-Grouse ✓	Murphy's Petrel*	Wandering Tattler
Olive-sided Flycatcher ✓	Black-vented Shearwater*	Guadalupe Murrelet*	Parkinson's Petrel*	Whimbrel
Red-headed Woodpecker ✓	Black Rail*	Harris's Sparrow	Pectoral Sandpiper	Whiskered Auklet*
Rock Sandpiper	Black Rosy-Finch*	Heermann's Gull*	Pinyon Jay ✓	Yellow-billed Loon
Snowy Owl	Black Scoter	Henslow's Sparrow	Prairie Warbler	Yellow-billed Magpie
Surfbird	Bobolink	Hudsonian Godwit	Red-faced Cormorant	Yellow Rail*
Thick-billed Longspur	Bristle-thighed Curlew*	Ivory Gull*	Red-legged Kittiwake*	
Western Grebe	Brown-capped Rosy-Finch*	King Eider	Ruddy Turnstone	
Wilson's Plover				
Wood Thrush				

These Tipping Point species are on a trajectory to lose another 50% of their remnant populations in the next 50 years if nothing changes.

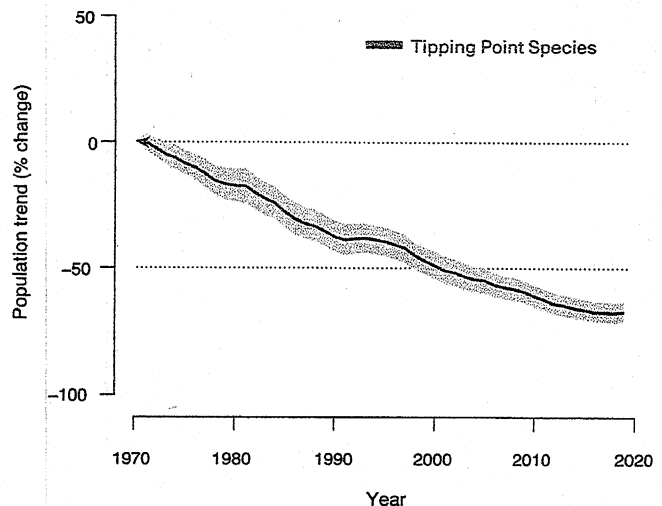
These 90 bird species lost 50% or more of their populations during 1970–2019. The Tipping Point species are on a trajectory to lose another 50% of their populations in the next 50 years (39 species), or already have perilously small populations and continue to face high threats, but lack sufficient monitoring data (31 species, indicated with an asterisk). For the USFWS Birds of Conservation Concern list, visit [fws.gov/media/birds-conservation-concern-2021.pdf](https://www.fws.gov/media/birds-conservation-concern-2021.pdf).

The Next Set of Species Plummeting Toward Endangered Status

Of the 1,093 bird species protected under the Migratory Bird Treaty Act, 89 birds have received additional protections as either threatened or endangered under the U.S. Endangered Species Act to prevent their extinction.

The Tipping Point species represent another 70 birds that could be next to face threatened or endangered status. Cumulatively, the Tipping Point species that have sufficient data for monitoring have lost more than two-thirds of their populations in the past 50 years.

Tipping Point species come from varied habitats, but they all have the same urgency—immediate science and conservation actions are needed to turn around declines.



70 Tipping Point Species

Urgent action is needed to help these birds before they become endangered.

GRASSLAND BIRDS

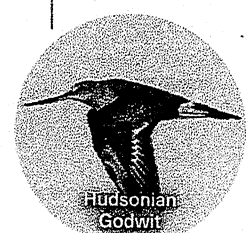
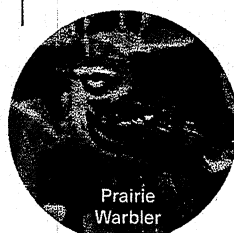
Prairie specialists such as Mountain Plover, Sprague's Pipit, and Chestnut-collared Longspur have lost more than 75% of their populations since 1970.

FOREST BIRDS

The steepest declines among forest birds include species that specialize on tree seeds (e.g., Pinyon Jay), long-distance migrants (e.g., Bicknell's Thrush), and aerial insect-eating specialists (e.g., Chimney Swift).

ARCTIC & ALPINE TUNDRA

Shrinking habitats due to changing climate and resource extraction threaten Arctic-breeding shorebirds (e.g., Hudsonian Godwit and Whimbrel) and alpine birds (e.g., Black Rosy-Finch).



COASTAL & OCEANIC

Nearly a quarter of seabirds found in U.S. waters are at risk of an Endangered listing, including murrelets, albatrosses, petrels, and shearwaters.

ARIDLAND BIRDS

Aridland birds are experiencing long-term declines, including Allen's Hummingbird, Bendire's Thrasher, and Greater Sage-Grouse.

WETLAND BIRDS

Though many waterbirds benefited from decades of wetland conservation, steep bird declines are still occurring in coastal saltmarshes (e.g., Saltmarsh Sparrow), freshwater marshes (e.g., Yellow Rail), and beaches (e.g., Least Tern).

*North Am. Bird Cons Initiative
2027. State of the Birds, US & Am
2027. State of the Birds, 0.00*

200 gr. 30
12.9%
vs 3.7 - 5

ECOLOGICAL IMPLICATIONS OF SAGEBRUSH MANIPULATION

A LITERATURE REVIEW

BY
JOEL G. PETERSON

WILDLIFE MANAGEMENT DIVISION
MONTANA FISH, WILDLIFE & PARKS

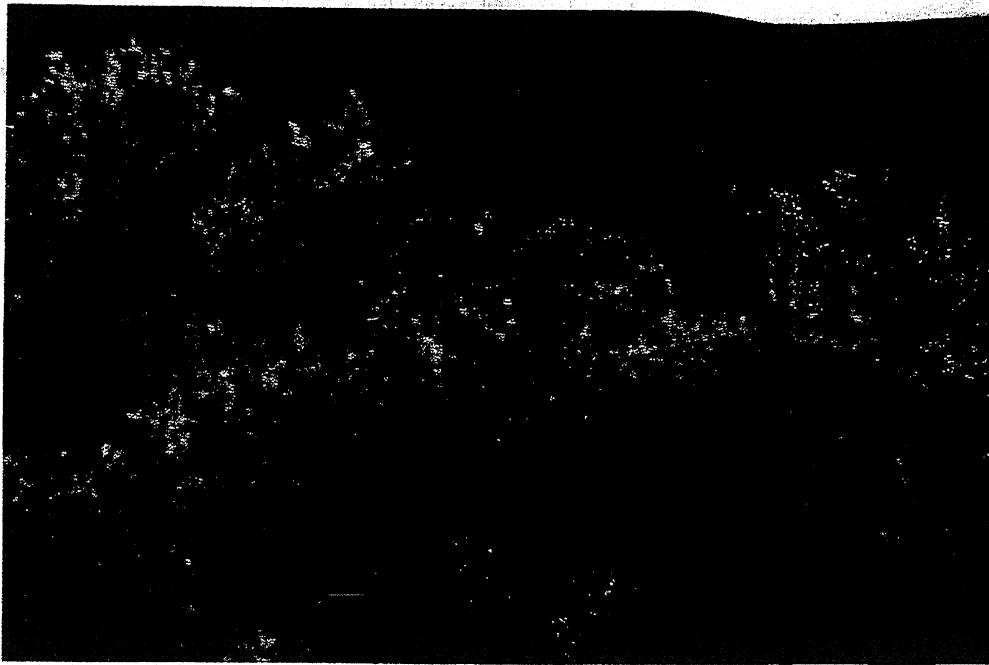
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1995

FORWARD

This report discusses the value of big sagebrush (*Artemisia tridentata*) to the ecosystem and explores potential consequences of its eradication. It is intended to bring into focus the importance of sagebrush habitats and to encourage land managers to consider all the potential ramifications of manipulation before implementing an action. It is not intended to discredit the use of vegetation manipulation when used as a tool that will clearly result in improved habitat. However, the Montana Fish, Wildlife & Parks (FWP) believes sagebrush manipulation is too often initiated without proper understanding of effects on wildlife, wildlife habitat and the overall ecosystem.



Elk in mountain big sagebrush near Gardiner, MT. (Photo by Carl Wambolt)

SAGEBRUSH: IMPORTANT FORAGE AND COVER FOR WILDLIFE



Mule deer fawn hiding under sagebrush canopy. (Photo by Randy Haight)

Sagebrush has been demonstrated to be a critical food source for several wildlife species during various seasons of the year, particularly fall, winter and spring. Cole (1955) found three different species of sagebrush comprised 93% of the winter diet of antelope in Montana. Shrubs (primarily sagebrush) are used almost exclusively by antelope from November through March and moderately through the other months (Pyrah 1987). Big sagebrush ranked first in mule deer diets in the Bridger Mountains of Montana during December, January and February (Wilkins 1956). During a 7-year period (1982-89), the average combined utilization for the various sagebrush species by deer and elk on the Gardiner, Montana, winter range was 59% for mountain big sage (*Artemisia tridentata* ssp. *vaseyana*), 42% for Wyoming big sage (*A. tridentata* ssp. *wyomingensis*), 32% for basin big sage (*A. tridentata* ssp. *tridentata*), and 16% for black sage (*A. nova*) (Wambolt 1990). Rouse (1957) found that three-tip sage (*A. tripartita*) received significant use by elk during severe winters. Sagebrush comprised 62% of the yearlong diet of adult sage grouse and essentially 100% of their winter diet in Montana (Wallestad et al. 1975). Field observations of the feeding behavior of the Pygmy rabbit (*Brachylagus idahoensis*) indicate heavy reliance on big sagebrush, primarily the seedheads and vegetative leaders. Published records of Pygmy rabbit food habits indicate 99% sagebrush in winter and 51% in summer (Green and Flinders 1980).



Elk Feeding on big sagebrush near Gardiner, MT. (Photo by Carl Wambolt)



The winter diet of the sagegrouse consists nearly 100% of sagebrush. (Photo by FWP)

Big sagebrush is a highly nutritious and digestible food source for big game animals such as mule deer (Peterson 1984). Although at one time it was speculated that deer avoid eating big sagebrush due to the monoterpenoids (volatile oils) contained in the foliage, research has shown otherwise (Peterson 1984, Bray et al. 1991). A particular variety of mountain big sagebrush (Hobble Creek) was preferred by wintering mule

deer in Utah over a non-monoterpenoid shrub, antelope bitterbrush (*Purshia tridentata*) (Welch et al. 1992). During winter, big sagebrush has a higher crude protein level and digestibility than most other shrubs or grasses. The winter crude protein level of sagebrush was 12.4% compared to only 3.7% for dormant grass and 10.6% for the highly preferred winter shrub, curl-leaf mountain mahogany (*Cercocarpus ledifolius*) (Welch and McArthur 1979). Digestibility of big sagebrush in winter ranged from 40-60% while bluebunch wheatgrass ranged from 43-50% (Ward 1971). The winter digestibility of grass was reported by the National Academy of Sciences (1964) to be 31%. Data from tests of browse and grass¹ species considering the above factors found only big sagebrush and curleaf mountain mahogany meet or exceed the protein needs of wintering mule deer (Thompson et al. 1973, Welch et al. 1979).



Mule deer rely heavily on sagebrush for winter forage in many areas of Montana.
(Photo by FWP)

Sagebrush also provides cover (nesting, resting and escape) for a wide variety of game and non-game species (i.e. protective cover for fawns, calves, nesting birds, grouse broods, etc.). As an example, Brewer's sparrows (*Spizella breweri*) nest off the ground in the foliage of big sagebrush plants (Best 1970). Research in Montana revealed that, during the breeding season, sage grouse utilize habitat with a canopy coverage of big sagebrush ranging from 20-50% (Eng and Schladweiler 1972, Wallestad 1972, Wallestad and Schladweiler 1974). Wintering grouse were found in an average of 28% sagebrush cover (Eng and Schladweiler 1972) and nesting birds in an average of 20-30% sagebrush cover (Wallestad and Pyrah 1974). Another species of special concern is the pygmy rabbit. The pygmy rabbit is limited to habitat types which contain tall dense sagebrush (Green 1980a, Green 1980b, Campbell 1982, Weiss 1984, Lyman 1991).

¹ Curleaf mountain mahogany (*Cercocarpus ledifolius*), chokecherry (*Prunus virginiana*), cliffrose (*Cowania mexicana*), bitterbrush (*Purshia tridentata*), juniper (*Juniperus spp.*), Gambel oak (*Quercus gambelii*), and dormant grass.



Brewers sparrow nest in foliage of big sagebrush. (Photo by FWP)

Sagebrush has other assets for wildlife in addition to forage and cover. Its thick canopy protects understory vegetation from livestock grazing. Understory vegetation can be a valuable food source for wildlife. Additionally, the crowns of sagebrush plants tend to breakup and weaken hard crusted snow on winter ranges making it easier for big game to access understory plants for foraging.

Plant physiologists at the Forest Service Intermountain Research Station's Shrub Sciences Laboratory in Provo, Utah, recognize big sagebrush as important wildlife food and cover, and are developing the best varieties for restocking rangelands (Tippets 1992).



United States
Department of
Agriculture

Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-229



Status and Management of Neotropical Migratory Birds

September 21-25, 1992
Estes Park, Colorado



Cowbird mgat

92

Management Implications of Cowbird Parasitism on Neotropical Migrant Songbirds

Scott K. Robinson¹, Joseph A. Grzybowski²,
Stephen I. Rothstein³, Margaret C. Brittingham⁴,
Lisa J. Petit⁵, and Frank R. Thompson⁶

- feed on
loggerhead
pds!

Abstract — Populations of brood parasitic Brown-headed Cowbirds (*Molothrus ater*) have increased to the point where they pose a potential threat to populations of many neotropical migrant songbirds. Because cowbirds mostly feed in short grass (e.g., pastures and lawns) or on bare ground (e.g., row crops), they benefit directly from human activities. Cowbirds commute up to 7 km between feeding areas and habitats where they search for host nests, often favoring forest edge or secondary growth. Several neotropical migrants with restricted geographical ranges are endangered, at least partly as a result of cowbird parasitism (e.g., Kirtland's warbler *Dendroica kirtlandii*, Black-capped Vireo *Vireo atricapillus*). Cowbird control using baited decoy traps has reduced the percent of nests parasitized, increased nesting success, and may be essential for the continued survival of these endangered species. It is not clear, however, whether cowbird trapping would be effective at a broader scale in reducing parasitism in extensively fragmented landscapes such as in the Midwest where many neotropical migrants are experiencing very high levels of parasitism. Cowbird trapping should be viewed as a stop-gap measure to protect specific endangered populations. We recommend instead the development of broader-scale approaches, perhaps in combination with local trapping. One approach to controlling cowbirds is landscape-level management such as consolidation of ownership to preserve large tracts, eliminating potential cowbird feeding areas within large tracts, and minimizing edge habitat. A second possible approach is large-scale cowbird eradication at winter roosts, but this approach may be too diffuse to help specific sensitive species or areas with high parasitism levels. Any management plan should be preceded by cowbird monitoring and preliminary data on levels of parasitism.

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BACKGROUND

Parasitism by the Brown-headed Cowbird (*Molothrus ater*) has become one of the major threats to populations of neotropical migrants on the breeding grounds (Mayfield 1977, Brittingham and Temple 1983). The Brown-headed Cowbird is a generalist brood parasite that lays its eggs in the nests of over 240 known host species (Friedmann and Kiff 1985), the majority of which are neotropical migrants. Historically, cowbirds were largely confined to the mid-continental prairies where they presumably followed herds of nomadic bison. Cowbirds mainly search for seeds and insects in short grass and on bare ground and may have depended upon grazing by large ungulates to create suitable feeding conditions. Since the clearing of forests for agriculture and the widespread introduction of livestock, however, cowbirds have expanded their geographical range eastward and westward as new feeding areas became available (Mayfield 1965). Similarly, cowbird populations have increased within their range as a result of increasing winter food supply (primarily waste grain in agricultural fields) and higher reproductive rates as cowbirds have come in contact with new hosts that lack defenses against parasitism (Mayfield 1965, Brittingham and Temple 1983). Cowbird populations have continued to increase in most sections of the United States (with the notable exception of the northeast: Robbins et al. 1986).

Increasing cowbird populations pose a potential threat to many hosts because of the cowbird's extraordinary fecundity and the extent to which cowbird parasitism reduces host productivity. Female cowbirds lay at least 30-40 eggs per season on average (Rothstein et al. 1986). Dan Roby (pers. comm.) found that individuals in captivity can lay up to 77 eggs in a season. Relatively small numbers of cowbirds can therefore parasitize many nests. Cowbird parasitism reduces host productivity for the following reasons: (1) female cowbirds remove host eggs (usually one) from 33% to 90% of all parasitized nests (Friedmann 1963, Weatherhead 1989, Sealy 1992); (2) cowbird eggs are unusually thick and, when laid, often break those of the host (Spaw and Rohwer 1987, Roskaft et al. 1990); (3) cowbird eggs have a short incubation period of 11 days compared with 12-14 days for most hosts (Nice 1953, Friedmann 1963), which gives nestling cowbirds a head start; (4) cowbirds usually parasitize hosts smaller than themselves, which gives cowbird nestlings a further advantage in competition with host young; and (5) cowbird nestlings grow faster, beg more loudly and have larger gapes than host nestlings (Friedmann 1929, Ortega and Cruz 1991). As a result of these factors, small hosts with long incubation periods usually fail to produce any of their own young if a single cowbird egg hatches (Rothstein 1975, May and Robinson 1985). For larger hosts and those with shorter incubation periods, cowbird parasitism is less costly (Smith 1981, Roskaft et al. 1990, Friedmann et al. 1977), except when the nests are multiply parasitized (i.e., two or more cowbird eggs are laid).

Neotropical migrants are especially vulnerable to cowbird parasitism. Most neotropical migrants build open-cup nests, which are the most frequent target of cowbirds (Friedmann 1929). The cowbird egg-laying period generally extends from mid-April until mid-July (Friedmann 1929, Scott 1963, Robinson, unpubl. data), which also coincides with the major period of egg-laying in most neotropical migrants (Whitcomb et al. 1981). Resident and short-distance migrants generally have longer breeding seasons that only partially overlap that of the cowbird.

Cowbird hosts with restricted geographical ranges can be particularly vulnerable to parasitism. Cowbird parasitism is considered one major cause (along with habitat loss) of population declines and the endangered status of the Kirtland's Warbler (*Dendroica kirtlandii*) (Walkinshaw 1983), Least Bell's Vireo (*Vireo belli pusillus*) (Franzreb 1989), Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Unitt 1987, Brown 1988), and Black-capped Vireo (*Vireo atricapillus*) (Grzybowski et al. 1986). Cowbird hosts with larger ranges may be less vulnerable because heavily parasitized populations can be "rescued" by immigrants produced from populations in areas where parasitism levels are lower. Local extinctions of wide-ranging species, however, have occurred in Oklahoma (Orchard Oriole, *Icterus spurius*) (J. Grzybowski, pers. obs.) and in the lower Rio Grande Valley (J. Arvin, pers. comm.) and may be linked to heavy parasitism.

The parasitic life history of cowbirds enables them to occupy a wider range of habitats than any other North American passerine. Because cowbirds do not tend their own offspring, their two main activities during the breeding season, feeding and searching for hosts, can be uncoupled and carried out in different locations. Cowbirds can therefore occupy habitats that fulfill only one of these needs (Rothstein et al. 1984) and regularly commute up to 7 km between feeding and nest-searching sites (fig. 1, see also Rothstein et al. 1984). In southern Illinois and central Missouri, for example, cowbirds that searched for nests in forests fed 0.1-4.0 km away in pastures, feedlots for livestock (pigs, horses, and cattle), mowed roadsides, lawns, recently plowed and planted row crop fields, campgrounds, gravel roadsides, bird feeders, and logging roads (fig. 1). In the Sierra Nevada of California, recently arrived cowbirds commuted on average once a day between horse corrals and feeding areas. Rothstein et al. (1984) estimated that this single corral made it possible for cowbirds to parasitize hosts over an area of 154 km² that contained no other suitable feeding sites.

In southern Illinois, where there are many potential feeding sites, cowbirds fed throughout the day (fig. 2). Perhaps because of the proximity of feeding and nest-searching areas, cowbirds tend to be most abundant in heterogeneous "fragmented" landscapes in which grassy areas are intermixed with shrubby old fields and/or forests. Cowbird control may be much more difficult in landscapes where human activities have created many potential feeding areas (Rothstein et al. 1987; see below).

away from these animals (Grzybowski 1990a). However, if livestock are dispersed, effectiveness is compromised (Rothstein et al. 1987, Tazik and Cornelius unpubl. data).

A modification of this approach has been used with rotational grazing systems, a system where cattle are moved from pasture to pasture on a rotational basis. At the Kerr WMA in Texas, cattle were placed immediately adjacent to Black-capped Vireo nesting areas (containing traps) at the beginning of the nesting season. Capture rates of females improved dramatically for the trap closest to the cattle, observed parasitism was the lowest recorded, and vireo reproductive success the highest (Grzybowski 1990b).

Capture rates at traps are often high at the beginning of the trapping effort, and drop substantially after an initial capture period of two to four weeks. Most of the cowbirds are normally removed in this initial period, although traps operated near cowbird feeding sites continue catching cowbirds for most of the season.

Cowbird Shooting

Female cowbirds can be attracted to taped calls and removed by shooting. Shooting has been used in conjunction with trapping on Fort Hood (Hayden and Tazik unpubl. data), but the specific effects of shooting were not isolated from those of trapping. About 247 female cowbirds were removed, some of which may have been later trapped if not shot. Nonetheless, the technique can be used to remove a substantial number of cowbirds, and may be useful and more cost-effective in some areas with small or scattered groupings of sensitive species. Cowbirds, however, are sensitive to activity near the traps, including extended human visitation. Thus, shooting should not be conducted at the trap locations themselves.

Control at Roosts

Because cowbirds gather in large roosts during the nonbreeding season, they are potentially vulnerable to large-scale control efforts (e.g., Johnson et al. 1980). Such control efforts, however, should be considered carefully before they are implemented. Previous eradication programs have had little apparent effect on national populations of cowbirds, possibly because birds from many regions gather in the same roosts. The effects of control at winter roosts are therefore likely to be diffuse and may not protect any specific endangered population. Control efforts may also work only for a few years if they select for cowbirds that avoid large roosts. Nevertheless, control at winter roosts may offer the most practical way to reduce cowbird populations in fragmented landscapes where local trapping is too expensive. Even if many of the cowbirds killed would be from areas where they pose little threat, the enhanced productivity of host species throughout their range might increase the pool of immigrants available to recolonize

areas with heavier rates of parasitism. Martin (1992), however, has argued that in most areas the effects of nest predation on host population dynamics far outweigh the consequences of brood parasitism. Landscape management that reduces both cowbird and nest predator populations (Temple and Cary 1988) may therefore still be the best long-term solution to preserving populations of neotropical migrants (see below). The ethical implications of large-scale eradication of a native songbird also need to be considered before such a program is considered. Even among the authors of this paper, opinions are divided about the value of control at winter roosts.

Landscape and Habitat Management

Perhaps the best and most permanent way to reduce the impact of cowbirds on neotropical migrants is through landscape-level management, which can be effective at a much larger scale than trapping. Because cowbirds are frequently associated with agriculture, human settlements, and internal and external edges, the best management strategy is to maintain large areas of contiguous habitat. Unfortunately, we cannot provide one specific guideline for minimum area requirements for reducing cowbird impacts because edge effects vary among landscapes and cowbirds can commute long distances when searching for nests (fig. 1). *As a general rule, however, bigger tracts are preferable to small ones, wider riparian strips are better than narrow ones, and compact shapes are preferable to complex shapes with high ratios of edge to interior.*

Managers must also keep in mind the landscape surrounding the area being managed. Landscapes with few feeding opportunities for cowbirds may not have problems with cowbird parasitism even along edges and small openings. Landscapes with abundant cowbird feeding habitat may have cowbird populations that saturate breeding habitat regardless of proximity to edge. Ultimate solutions to the increasing threat of cowbird parasitism to neotropical migrants must involve changing land-use practices and configurations that reduce cowbird feeding areas. Below we provide more specific guidelines.

Forest Habitat

1. Where possible, managers should seek to maintain and establish large areas of contiguous forest cover that include core areas of forest interior. Estimates of areas necessary to sustain populations of neotropical migrants vary regionally. Robbins et al. (1989), for example, suggest maintaining at least 3000 ha of contiguous forest as the minimum required to retain local populations of forest songbirds in the mid-Atlantic states. Data from moderately fragmented areas of the Midwest suggest that areas of 20,000-50,000 ha may be necessary because the landscape supports very high cowbird populations and parasitism rates remain high even two km from feeding areas (Robinson, unpubl. data). The Biological Advisory Team (1990)

[badkitty] Autopsy results..

From: Paul Sieracki via badkitty list (badkitty@groups.electricenseers.net)

To: badkitty@groups.electricenseers.net

Date: Monday, December 14, 2020, 09:06 AM MST

"The laboratory results are very informative but did not identify a single definitive cause of mortality.

Starvation, unexpected weather to blame in mass migratory songbird mortality

SANTA FE –The U.S. Geological Survey National Wildlife Health Center has analyzed representative samples of the migratory songbirds collected, cataloged and sent for analyses by New Mexico Department of Game and Fish biologists, in early September. The lab report indicates that the single abnormality shared by nearly all birds was body condition ranging from poor to severely emaciated.

Kerry Mower, the Department's wildlife disease specialist, said, "The laboratory results are very informative but did not identify a single definitive cause of mortality. However, they did find that nearly all birds were severely emaciated."

The single abnormality shared by nearly all birds was body condition ranging from poor to severely emaciated. These observations are evidence of physical exertion without nourishment to support recovery, including:

- the large breast muscles controlling birds' wings were severely shrunken;
- kidney failure was apparent in many of the birds;
- stomachs and intestines were empty of foodstuffs;
- many intestines contained small amounts of blood, which is one of the effects of starvation;
- fat deposits, the stored energy for migration, were depleted; and
- lung tissues were irritated.

The USGS National Wildlife Health Center, located in Madison, Wis., is renowned for the thoroughness of the diagnostic tests for wildlife disease diagnosis and management. The center conducted numerous tests during analyses, ruling out contagious bacterial disease, contagious viral disease including avian influenza and Newcastle disease and parasites as cause of death, as well as finding no evidence of smoke poisoning or pesticide poisoning.

From the lab reports, Department biologists know that migrating birds entered New Mexico in poor body condition and some birds were already succumbing to starvation. The unusual winter storm exacerbated conditions, likely causing birds to become disoriented and fly into objects and buildings. Some were struck by vehicles and many landed on the ground where cold temperatures, ice, snow and predators killed them.

"The Department would like to thank many partners and the public who reported mortalities across New Mexico," said Erin Duvvuri, the Department's avian biologist. "Hundreds of reports were received through email, phone calls and the iNaturalist app." Reports declined by late September.

The Department would also like to thank all of the partner organizations who were essential to this process. Partners include the: United States Fish and Wildlife Service, White Sands Missile Range, United States Forest Service, Bureau of Land Management, New Mexico Avian Conservation Partners, New Mexico State University, University of New Mexico, Audubon Southwest, Los Alamos National Laboratories and the New Mexico Wildlife Center.

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Sagebrush and ungulate relationships on Yellowstone's northern range

Carl L. Wambolt

Abstract Sagebrush (*Artemisia* spp.) ecology and forage relationships with ungulates are related to the Northern Yellowstone Winter Range (NYWR). The NYWR in northern Yellowstone National Park (YNP) and adjacent Montana is an important area for ungulates. I synthesized research published in peer-refereed and peer-edited literature related to the historical and present associations between ungulates and sagebrush on the NYWR. The NYWR habitats preferred by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) were dominated by sagebrush, and these ungulates preferentially foraged on 4 sagebrush taxa. There were significant differences in development between protected and browsed sagebrush at 19 locations across the NYWR. Elk foraging on sagebrush significantly increased utilization and held sagebrush populations below their potential in the absence of other browsing ungulates. Sagebrush had not recovered from burning 10–19 years earlier. Knowledge of sagebrush taxa should provide resource managers important information for management of the extensive NYWR habitats.

Key words *Artemisia tridentata*, big sagebrush, *Cervus elaphus*, elk, mule deer, *Odocoileus hemionus*, winter range, Yellowstone

Big sagebrush (*Artemisia tridentata*) taxa are dominant on the largest vegetation type of the Northern Yellowstone Winter Range (NYWR; Houston 1982). These taxa are particularly important in portions of the NYWR that are relatively free of snow and thereby accessible for ungulate foraging throughout winter. Twentieth-century naturalists (Rush 1932; Wright and Thompson 1935; Cahalane 1943; W. H. Kittams. Sagebrush on the lower Yellowstone range as an indicator of wildlife stocking, Yellowstone Natl. Park files, unpubl. rep., Wyo., 1950) have commented on the conspicuous use of sagebrush for forage and cover by ungulates, primarily elk (*Cervus elaphus*), on the NYWR and expressed concern over what they considered excessive use of sagebrush in the winter diets of ungulates at Yellowstone National Park (YNP).

The effects of Yellowstone's large populations of ungulates on sagebrush taxa on the NYWR have been debated for ≥70 years (Rush 1932, Wright and Thompson 1935). Debate has also centered on other species of woody plants like aspen (*Populus tremuloides*) and

willows (*Salix* spp.). However, the National Park Service (NPS) was concerned enough about sagebrush and other browse on the NYWR that they constructed 10 2-ha exclosures on the NYWR in 1957 and 1962 to investigate the relationships between ungulate foraging and plant communities. Eight of the exclosures still exist; 4 contain only sagebrush habitats, and 4 contain large areas within sagebrush habitats.

The NPS (YNP 1997) stated that big sagebrush is holding its own or increasing on 97% of the NYWR, and the decline in sagebrush on the other 3% is a departure from prehistoric conditions or an artifact of past human activities, such as livestock grazing. However, published research, absent before 1987, has confirmed that concerns of early naturalists about sagebrush habitat were well based. Those investigations determined the mechanisms that influence sagebrush–herbivore interactions on the NYWR and their effects. I synthesized the peer-refereed and peer-edited literature on the NYWR that has investigated aspects of sagebrush ecology and forage rela-

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tionships with ungulates. This information should be useful in understanding effects of different management strategies on the NYWR and similar areas.

The Northern Yellowstone Winter Range

The NYWR occupies approximately 100,000 ha over an 80-km stretch along the lower elevations in northern YNP and extends northward into Montana along the Yellowstone River drainage (Fig. 1; Houston 1982). The Lamar and Gardiner rivers also drain portions of YNP lowlands that are relatively free of snow, thereby providing a reliable winter location for foraging ungulates (Houston 1982). Singer (1991) reported that 80% of the ungulates in YNP during winter were found on the NYWR. In addition, $\geq 2,544$ Rocky Mountain mule deer (*Odocoileus hemionus*) and 8,626 Rocky Mountain elk have wintered on the portion of the NYWR north of the YNP boundary in Montana during the last decade (T. Lemke, Mont. Fish, Wildl. and Parks, unpubl. data).

The generally favorable climate for ungulate winter foraging varies across the NYWR. P. E. Farnes (SCS, Mean annual precipitation for Yellowstone National Park, unpubl. map, Bozeman, Mont., 1975) reported approximately 280 mm of annual precipitation at Gardiner, Montana (1,616 m), 400 mm at Mammoth (1,899 m), and 410 mm at Tower Falls (1,912 m). Fifty percent of the precipitation is received as snow, although peak moisture occurs in spring and early summer (Farnes 1991). Soils on the sagebrush habitats have

been described by Lane (1990) as typical calciborolls, aridic haploborolls, and aridic calciborolls. The Boundary Line Area (BLA) near Gardiner, Montana (Fig. 1) is located on ancient mudflows that are higher in clay and lower in fertility than the rest of the area.

The area surrounding Gardiner, Montana known as the Gardiner Basin, which includes the BLA, has less snow than the majority of the NYWR that lies to the east in YNP. The Gardiner Basin is particularly important for pronghorn (*Antilocapra americana*) in the BLA portion and mule deer throughout. Elk are able to negotiate the deeper snow at higher elevations in the remaining portions of the NYWR. The natural winter range provided by the Gardiner Basin is created by the orographic effects on precipitation of mountain peaks $\leq 3,353$ m. Ideal winter range on extensive south- or west-facing aspects in the Gardiner Basin have been influenced by glacial scouring, morainal deposition, and outwash sediments.

Elk are the only browsing ungulate found in large numbers during winter on the remaining portions of the NYWR within YNP (Singer and Renkin 1995). Bison (*Bison bison*) are an important herbivore over the NYWR, but no evidence exists that bison have had a direct impact on the shrubs of sagebrush habitats.

Big sagebrush is the largest vegetation type on the NYWR. Big sagebrush taxa are dominant over 22% of the NYWR (Houston 1982). More important, sagebrush is the dominant vegetation form on the portions of the NYWR that are most valuable as winter range for ungulates (DeSpain 1990). Additionally, sagebrush communities often furnish security and thermal cover for ungulates and other animals (Wambolt and McNeal 1987). The sagebrush habitats found within the NYWR include the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bluebunch wheatgrass (*Agropyron spicatum*) type that is found primarily at lower elevations in the Gardiner Basin. Over the rest of the NYWR the mountain big sagebrush (*A. t. vaseyana*)-Idaho fescue (*Festuca idahoensis*) habitat type dominates (Wambolt and Sherwood 1999). Other sagebrush are the basin big sagebrush (*A. t. tridentata*) and black sagebrush (*A. nova*). Important plants include the sprouting shrubs usually associated with sagebrush habitats, specifically rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidifolius*).

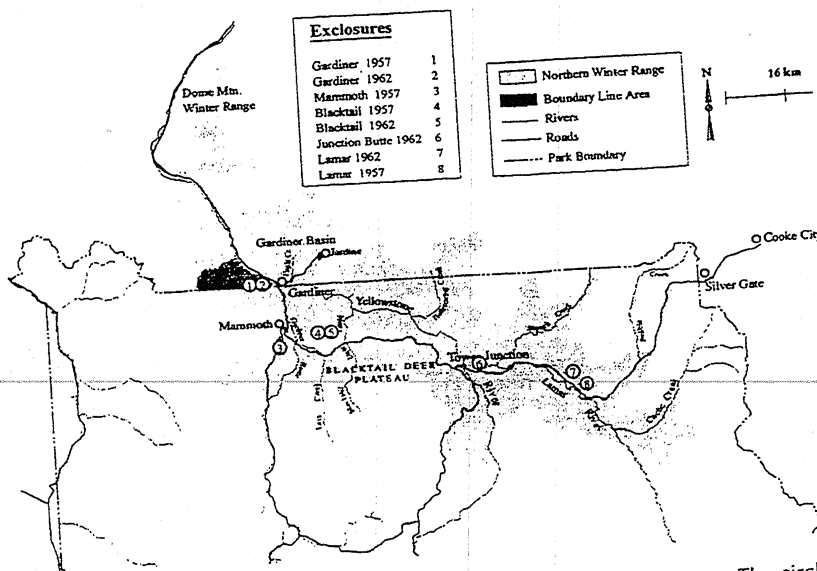


Fig. 1. The Northern Yellowstone Winter Range, Montana and Wyoming. The circled numbers represent locations of the exclosures constructed in 1957 and 1962 that still exist. National Park Service map.

Table 1. Crude protein (%) of bluebunch wheatgrass dry matter by cattle-grazing treatment and season, averaged over a 3-year study (Wambolt et al. 1997).

Grazing treatment	Crude protein (%)			
	Spring	Summer	Fall	Winter
Spring	11.4A*	6.8A	4.6A	3.2A
1-year rest	10.0B	5.9B	3.8B	2.9A
Long-term rest	9.6B	5.5B	3.3C	2.9A

* Means differ ($P \leq 0.05$) among grazing treatments within each season when followed by a different letter.

florus), and gray horsebrush (*Tetradymia canescens*) found throughout the NYWR. Other important grasses are prairie junegrass (*Koeleria macrantha*) and Sandberg bluegrass (*Poa secunda*).

Sagebrush forage relationships on the NYWR

Sagebrush taxa are highly nutritious and preferred forage for ungulates (Welch and McArthur 1979). They have been bred and selected to improve the forage values of rangelands (Welch and Wagstaff 1992). Sagebrush is particularly high in protein. Welch and McArthur (1979) found the mid-winter crude protein content of 21 big sagebrush accessions averaged 12.4% (range = 10–16%). Grasses incur a large drop in protein and other nutrients during winter. Wambolt et al. (1997) found that during fall and winter in southwestern Montana, bluebunch wheatgrass, the dominant grass of relatively snow-free portions of the NYWR, does not meet the minimum protein levels required for elk (Nelson and Leege 1982). Bluebunch wheatgrass did not meet protein gestation requirements for elk during the gestation period (Table 1). Even in summer, when protein content was highest, bluebunch wheatgrass did not meet elk lactation requirements by August. Wambolt et al. (1997) discussed why elk would be physically unable to consume enough bluebunch wheatgrass to meet protein-maintenance requirements during winter, which are significantly less than requirements for production. The winter nutritional deficiencies of grasses, contrasted to sagebrush, explain why sagebrush is an important forage on the NYWR (Welch and McArthur 1979). The concerns of Nagy (1979) regarding inhibitory effects of sagebrush volatile oils on ruminant digestion have been proven unimportant under natural circumstances. When sagebrush is browsed, the highly volatile compounds are lost with minimal influence on digestion (Cluff et al. 1982, White et al. 1982).

The effects of secondary compounds from the

NYWR sagebrush taxa have been studied in detail. The influence of crude terpenoid content on in vitro organic matter digestibility (IVOMD; Striby et al. 1987) and preference (Personius et al. 1987, Bray et al. 1991) by mule deer was determined for 4 sagebrush taxa in the Gardiner Basin. The order of increasing digestibility among taxa was black sagebrush, mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, respectively (Table 2; Striby et al. 1987). Sagebrush IVOMD generally increased from January to April as crude terpenoids decreased. Although extraction of crude terpenoids from sagebrush foliage did increase IVOMD, it resulted in few differences in IVOMD among taxa and collection dates during the winter (Striby et al. 1987). Striby et al. (1987) found no significant differences in sagebrush digestion among wild NYWR mule deer or domestic sheep and steers. Therefore, it appears that no significant differences would exist in mule deer, elk, and pronghorn found on the NYWR.

From 31 compounds isolated from sagebrush, Personius et al. (1987) selected 7 by discriminant analysis as preference indicators among the 4 taxa. Seven other compounds were useful for separating individual plants within a taxon into browse form classes. Bray et al. (1991) used the compounds selected by discriminant analysis to differentiate preference among taxa in conducting a mule deer feeding trial to determine if deer would discriminate against forage

Table 2. In vitro organic matter digestibility (IVOMD; %) of 4 sagebrush taxa at 3 dates on the NYWR using wild mule deer, sheep, and steer inoculum (Striby et al. 1987).

Taxon	IVOMD		
	1 Jan	15 Feb	1 Apr
Mule deer			
Black sagebrush	37.6AE*	45.3AF	46.2AF
Mountain big sagebrush	45.8BE	47.9AE	53.5BF
Wyoming big sagebrush	46.0BE	49.5AE	57.4BCF
Basin big sagebrush	47.2BE	63.4BF	62.4CF
Sheep			
Black sagebrush	41.5AE	44.7AF	50.4AG
Mountain big sagebrush	45.4BE	48.5BF	52.7AG
Wyoming big sagebrush	50.3CE	52.5CF	58.1BG
Basin big sagebrush	54.0DE	55.3DE	59.6BF
Steer			
Black sagebrush	42.4AE	42.8AE	47.0AF
Mountain big sagebrush	48.3BE	52.0BF	53.0BF
Wyoming big sagebrush	50.5CE	53.7BF	57.8CG
Basin big sagebrush	55.8DE	56.6CE	58.4CE

* Means among taxa differ ($P \leq 0.05$) within date and inoculum source when followed by a different letter (A, B, C, D). Means among dates differ ($P \leq 0.05$) within taxon and inoculum source when followed by a different letter (E, F, G).

treated with these compounds individually. Mule deer selected significantly higher quantities of untreated forage with each compound tested. Personius et al. (1987) and Bray et al. (1991) found that volatility of compounds had little influence on preference at the concentrations found in nature. Volatile compounds and nonvolatile sesquiterpene lactones were responsible for deterring foraging. This research (Personius et al. 1987, Bray et al. 1991) has explained the major role that plant chemistry plays in determining sagebrush palatability and, thus, preference by herbivores.

Wambolt and McNeal (1987) determined site characteristics for elk and mule deer foraging on the NYWR. Elk were physically capable of using most regions of the Gardiner Basin including timbered areas. Yet their most intensive feeding activity was in mountain big sagebrush habitats with relatively abundant grass, at least partially due to a decline in sagebrush from long-term heavy browsing (Rush 1932, Wright and Thompson 1935, Wambolt 1996, Wambolt and Sherwood 1999). Mule deer preferred areas with Wyoming big sagebrush cover adjacent to steep and dry topography at lower elevations. Such areas furnished security and thermal cover while meeting forage requirements. The distribution and concentrations of elk on the NYWR vary with wind, snow, temperature, and crusting that expose or conceal forage (Greer et al. 1970, Houston 1982). North of the YNP boundary, hunting affects animal distribution on the NYWR (Houston 1982, Wambolt 1996). On the lower portions of the Gardiner Basin, elk are not present as consistently as mule deer because elk hunting occurs from autumn through late winter. This is especially true during open winters when elk can forage within the security of YNP (Houston 1982, Farnes 1991). When elk are forced by forage limitations to leave the security of YNP, the number of elk harvested during Montana's special late hunting season (mid-Dec through Feb) in the area is a good index of winter severity. This elk harvest is positively correlated to use of sagebrush leaders by taxon (Wambolt 1996). Foraging on sagebrush increases when more elk are forced from higher elevations during severe winters (Greer et al. 1970, Wambolt 1996). Under these conditions the selectivity of browsers for certain subspecies of sagebrush is minimized (Wambolt 1996).

Wambolt (1996) established preferences by mule deer and elk for the 4 sagebrush taxa discussed previously over 10 winters of varying severity in the Gardiner Basin. The purpose of the 10-year length of the study was to avoid conclusions from anomalies that can occur for shorter periods. Each year approxi-

mately 2,500 leaders were tagged on 244 plants to later determine if winter browsing had occurred. Mule deer and elk browsed very substantial amounts of the 4 sagebrush taxa. Mule deer diets averaged 52% big sagebrush over the 10-year study as determined by microhistological techniques (Sparks and Malechek 1968) on composite samples of feces collected early each spring. During the study, no 1 year was significantly above average in severity of temperature or snow depth compared to the long-term average (Farnes 1991). Mule deer and elk displayed distinct preferences among the 4 taxa. The percentage of total tagged sagebrush leaders used during a given winter reached 91% for mountain big sagebrush, the preferred taxon that averaged 56% utilization at the study sites over the 10-year study. Wyoming big sagebrush was narrowly preferred (39%) over basin big sagebrush (30%). Black sagebrush was least preferred (17%). These long-term preferences supported the findings of Personius et al. (1987) and Bray et al. (1991) regarding sagebrush terpenoid content and its affect on herbivory.

Wambolt et al. (1994) developed regression models that avoid colinearity problems of earlier models and accurately predict production of winter forage for the 3 big sagebrush subspecies on the NYWR. Previous modeling of forage production from big sagebrush had not considered possible subspecies differences or different browsing histories that affect shrub morphology. The consideration of taxon and form class resulted in an average increase of 10% in R^2 values to 0.90 (Wambolt et al. 1994). The models facilitate determination of carrying capacity, detecting trends in forage production, and measuring plant response to management. They also emphasized the importance of taxon recognition and the role of past browsing history on present forage production.

Big sagebrush status on the NYWR

Hoffman and Wambolt (1996) tested the hypothesis that Wyoming big sagebrush plants protected from browsing for 35 years would exhibit growth characters similar to browsed plants. They made paired comparisons in and out of a 2-ha NPS exclosure erected in 1957 (Fig. 1; Gardiner 1957). Because of heavy browsing, plants outside the exclosure had no terminal leader growth. The plants inside the exclosure were dominated by terminal growth, and axial long shoots were rare. Thus, for further investigation, it was necessary to compare the terminal leaders of protected plants inside the exclosure to axial long shoots on browsed plants. Unbrowsed plants



Fig. 2. A Wyoming big sagebrush killed by browsing in the Gardiner Basin, 19 June 1998. The sizable trunk, but small plant size, indicates this plant experienced heavy use for years before dying.

had consistently higher production than browsed plants. The average production per plant was 10 g with browsing and 45 g with protection. No measurements of dead crown were taken, but plants under protection appeared vigorous, whereas plants outside the enclosure had large amounts of dead crown (Fig. 2).

The greatest difference between browsed and unbrowsed plants was in seedhead production. Seedheads averaged 0.08 per browsed plant, and 60.3 per unbrowsed plant (range = 0–3). Related studies confirm that stress, such as herbivory, may delay or prevent flowering for several years (McConnell and Smith 1977, Bazzaz et al. 1987, Maschinski and Whitham 1989). The lower overall production of browsed sagebrush plants (Hoffman and Wambolt 1996) indicates that foliage loss results in reduced reproductive potential. Bilborough and Richards (1991) found that buds for flowering stems on mountain big sagebrush were located on short shoots at the distal end of the terminal leader. Because almost all terminal leaders were removed on browsed plants (Hoffman and Wambolt 1996), flowering stems would have to be initiated from elsewhere. The loss in seedhead production from browsing on the NYWR has undoubtedly resulted in declines in reproduction for sagebrush as the taxon lacks any asexual means of reproduction.

The addition of average seedhead weight improved the capability of models to predict production of winter forage from the 3 NYWR big sagebrush subspecies (Wambolt et al. 1994). Improved models were used when the 3 taxa exhibited light use (browse form class). Heavily used plants produced few inflorescences; therefore, the addition of average

seedhead weight to the model was most useful for predicting forage production from low-use plants. The segregation of browse form classes and inclusion of average seedhead weight in the models acknowledge the impact browsing has had on the annual production and reproduction of NYWR sagebrush and compliment Hoffman and Wambolt (1996).

Although snow cover is relatively light on the NYWR, some snow falls each winter and may protect small sagebrush plants for several years before ungulates find them available for foraging. Nearly half (47%) of the mountain big sagebrush plants that were established between 1978 and 1992 germinated in 1988, when Yellowstone had numerous fires. That year offered relatively good seed production due to plentiful spring moisture, followed by a winter with considerably more snow than typical through the 15-year period. The snow protected the seedlings from herbivory. Those conditions coincided with a 35–40% reduction in elk, due to the most severe winter (1988–1989) of the period, that allowed the seedlings to establish during the next several years of reduced numbers of elk (T. Lemke, Mont. Fish, Wildl. and Parks, unpubl. data).

Big sagebrush taxa are not tolerant of fire. Fire on NYWR sagebrush habitats has been an additive injury, along with intense herbivory, to sagebrush. Mehus (1995) studied a wildfire in the Gardiner Basin to determine how much reestablishment of sagebrush and rabbitbrush taxa had occurred under continuous browsing. Nineteen years after the fire, recovery in canopy cover was at levels between 1 and 20% of that of the 3 big sagebrush subspecies in adjacent, unburned sagebrush stands, which were already in decline from historically heavy browsing (Houston 1982, Wambolt 1996, Wambolt and Sherwood 1999). Wyoming big sagebrush recovered to a lesser extent than mountain or basin big sagebrushes. Similar relationships were found for big sagebrush density and production.

Hoffman (1996) studied 7 prescribed burns conducted 10–14 years earlier by the U.S. Forest Service on mountain big sagebrush sites in the Gardiner Basin. These burns were compared with 33 unburned sites to determine recovery following burning. Sagebrush canopy coverage and densities on unburned sites averaged 12 and 15 times, respectively, greater than on burned sites. Mehus (1995) and Hoffman (1996) confirmed that burning accelerates the browsing-induced decline (Houston 1982, Wambolt 1996, Wambolt and Sherwood 1999) of NYWR sagebrush. In addition to directly eliminating sagebrush, fire concentrates browsing on surviving or reestablishing shrubs.

Killed
by
fire.

Thirty-five percent of mountain big sagebrush plants were killed by heavy browsing (Fig. 2) between 1982 and 1992 (Wambolt 1996). Many surviving plants developed a heavy-use browse form class with a high percentage of dead crown. The dead crown in the 3 big sagebrush subspecies increased in proportion to the overall amount of browsing received by each taxon. The percentage of dead crown in live plants for mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, was 58.7, 45.4, and 30.1%, respectively (Wambolt 1996).

The 10-year average browsing level of 56.1% on mountain big sagebrush north of YNP may be above the level that can be sustained (Wambolt 1996). Bilbrough and Richards (1993) confirmed that this level of use could inflict heavy damage on sagebrush when they reported that sagebrush was not efficient in compensatory growth following heavy winter browsing. In general, plants with evergreen leaves depend more on those leaves for storage than do plants with deciduous leaves (Bryant et al. 1983). Sagebrush carries 50% of its nitrogen (N) and total nonstructural carbon (TNC) pool in its leaves (Bilbrough 1990); each time a leaf is removed, the N and TNC it contains is lost to the plant.

Wambolt and Sherwood (1999) considered the effect of herbivory on sagebrush across the NYWR. They compared parameters between shrubs that were browsed by ungulates or protected since NPS exclosures were constructed in 1957 and 1962. Their measurements were taken in (protected) and near (browsed) the 6 NYWR exclosures (Fig. 1) that were not burned during the Yellowstone fires of 1988. Because the 2-ha exclosures contained considerable environmental variation, the sagebrush habitat within each exclosure was stratified (Hurlbert 1984) by separating topographic, soil, and microclimatic variation into 19 paired sites. With random sampling using paired sites, (in and out of the exclosures) it is unlikely that comparable distributions of topographic positions would have been obtained, regardless of sample size (Coughenour 1991). Predictably, Wambolt and Sherwood (1999) obtained different results than did Singer and Renkin (1995) sampling at the same locations. Singer and Renkin (1995) used randomly placed plots as warned against by Hurlbert (1984), and obtained smaller samples of <8% of the transect area the first 5 years and 23% the last 2 years of that sampled by Wambolt and Sherwood (1999).

Wambolt and Sherwood (1999) found a significant difference between the development of protected and browsed big sagebrush communities (Table 3). Wambolt and Sherwood (1999, In press) stated, "Since the period of exclosure construction in 1957 and 1962, there has been a significant difference in

Table 3. Percent canopy cover of big sagebrush at 19 environmentally paired sites either browsed or protected. The paired sites are associated with the exclosures established either in 1957 or 1962 (Wambolt and Sherwood 1999).

Site	Canopy cover (%)		
	Protected	Browsed	Probability > t^a
Mammoth-57	49.5	28.7	0.0004
Junction Butte-62A	31.9	11.6	0.0000
Junction Butte-62B	32.1	11.5	0.0001
Lamar-57A	3.2	0.1	0.0291
Lamar-57B	2.9	0.1	0.0002
Lamar-57C	44.3	19.8	0.0004
Lamar-57D	25.4	16.9	0.0015
Lamar-62A	9.3	1.3	0.0005
Lamar-62B	29.6	8.2	0.0001
Lamar-62C	41.7	9.3	0.0004
Lamar-62D	42.1	9.7	0.0000
Gardiner-57A	3.9	0.0	0.0001
Gardiner-57B	3.6	0.1	0.0004
Gardiner-57C	4.5	1.1	0.0001
Gardiner-57D	1.4	0.4	0.0073
Gardiner-62A	21.8	0.4	0.0001
Gardiner-62B	17.6	4.3	0.0000
Gardiner-62C	2.4	0.2	0.0012
Gardiner-62D	6.8	0.0	0.0001

^a The comparative P value for similar inferences is 0.0027.

the development of protected and browsed big sagebrush communities. Average big sagebrush canopy cover on protected sites was 202% greater ($P \leq 0.0027$) than on browsed sites over the 19 paired sites. The average big sagebrush cover for all 19 sites was 19.7% inside and 6.5% outside the exclosures. This relationship was universal on sites with Wyoming big sagebrush or mountain big sagebrush, flat to very steep topographies, and all aspects and precipitation levels."

The Wyoming big sagebrush sites under protection averaged almost 10 times more sagebrush cover than where browsing had continued following exclosure construction (Fig. 3). Mountain big sagebrush cover was almost 3 times as great where protected (Fig. 4). Ungulate browsing also affected numbers of big sagebrush plants. Across the NYWR big sagebrush plants were twice as numerous with protection as with browsing. There was an average density of 30.5 plants/60 m² inside and 15.3/60 m² outside the exclosures. Individual mountain big sagebrush plants produced 88% more winter forage where protected across the NYWR (Wambolt and Sherwood 1999). The production differential for Wyoming big sagebrush was even greater, but because browsed plants were so reduced in size, their growth parameters were not suitable for production models (Wambolt et



Fig. 3. At the Gardiner (constructed in 1957) enclosure, near Gardiner, Montana, 19 June 1998. The foreground without sagebrush is outside the enclosure while a thriving stand of Wyoming big sagebrush inside the enclosure shows the recovery that has occurred since the long period of overuse before enclosure construction. The recovery illustrates the site's potential.

al. 1994). The response of the sprouting shrubs (green rabbitbrush, rubber rabbitbrush, and gray horsebrush), as measured by canopy cover and density, was similar to that of big sagebrush across the NYWR.

Singer and Renkin (1995) and Wambolt and Sherwood (1999) found a large impact from browsing on the Wyoming big sagebrush in the Gardiner Basin (Fig. 3). Wambolt and Sherwood (1999; In press) considered the difference in impact between Wyoming big sagebrush and mountain big sagebrush (Fig. 4) with this statement: "Pronghorn and mule deer often forage heavily on big sagebrush taxa (Welch and McArthur 1979). Mule deer diets averaged 52% big sagebrush over a 10-year period (Wambolt 1996) only a couple of kilometers away from the 8 Wyoming big sagebrush paired sites. A high degree of utilization is reflected in the great impact on Wyoming big sagebrush populations at these 8 sites where elk may also be present with pronghorn and mule deer (Singer and Renkin 1995). However, as Singer and Renkin (1995) point out, elk are the only significant browsers at the other 11 paired sites due to excessive snow depths. Therefore, with our findings, it becomes obvious that elk numbers were large enough on the NYWR for a sufficient number of years before enclosure construction started in 1957 to greatly reduce big sagebrush populations."

Wambolt (1996) concluded that any of the 4 NYWR sagebrush taxa would be heavily browsed if severe winter conditions precluded ungulates from exercising their preferences. However, mountain big sagebrush was clearly the preferred taxon by mule deer and elk. The fact that Singer and Renkin (1995) and

Wambolt and Sherwood (1999) found Wyoming big sagebrush to be more impacted than mountain big sagebrush was a function of snow depth limiting pronghorn and mule deer foraging over the larger distribution of mountain big sagebrush.

Conclusion

Big sagebrush is the native dominant on the large portion of the NYWR considered most important for ungulates (Houston 1982, DeSpain 1990). Although NYWR sagebrush ecology and forage relationships with ungulates has been a concern since the 1920s, no peer-reviewed research on the topic had been published prior to 1987. The historical evidence and recent studies (Patten 1993, Hoffman and Wambolt 1996, Wambolt 1996, Wambolt and Sherwood 1999) indicate a significant decline of NYWR sagebrush. This potentially impacts ungulates that rely on sagebrush habitat for meeting their nutritional needs and other requirements. Species, such as mule deer, with well-documented reliance on sagebrush, have already been impacted. Singer and Renkin (1995) related a 66% decline in mule deer using the lower elevations of the NYWR over the 2 decades previous to their study to be likely due to a decline in Wyoming big sagebrush. I agree with this assumption because, despite decades of both sagebrush and mule deer declines in the Gardiner Basin (outside YNP), mule deer diets averaged 52% big sagebrush over a climatically mild 10-year period during which sagebrush continued to decline (Wambolt 1996). However, elk are the only significant browser on 97% of the sagebrush habitats on the NYWR (YNP 1997). Therefore, elk browsing is responsible for sagebrush declines over



Fig. 4. At the Lamar (constructed in 1957) enclosure, near the confluence of Soda Butte Creek and the Lamar River, 19 June 1998. The foreground without sagebrush is outside the enclosure and the heavy growth of mountain big sagebrush beyond the fence is inside the enclosure. The Lamar River is seen downslope in the distance.

most of the NYWR (Wambolt and Sherwood 1999). As noted in 1 report, "Because elk are so much more abundant than pronghorn on the northern range, even very low consumption rates of sagebrush by individual elk could result in a large cumulative amount of sagebrush consumed" (YNP 1997). Elk are impacted as the loss of their highest winter protein source (sagebrush) continues (Welch and McArthur 1979). This loss will manifest itself in a decreasing ability of elk to meet their nutritional needs and requirements for reproduction. But, whatever the long-term consequences to the elk herds that have been unmanaged inside YNP since the adoption of the Natural Regulation policy by YNP in 1968 (Houston 1982), the implications for other organisms are clear. In concert with the decline of the native vegetation (sagebrush and dependent species), it is reasonable to expect that numerous animals (Welch 1997), in addition to mule deer, relying on sagebrush habitats will also be impacted. The information available on NYWR sagebrush should provide an understanding of important relationships and management opportunities in YNP and elsewhere.

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Associate Editor: Krausman

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GREATER SAGE-GROUSE

*Ecology and Conservation
of a Landscape Species and Its Habitats*

Steven T. Knick and John W. Connelly, *Editors*

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CHAPTER EIGHTEEN

Factors Associated with Extirpation of Sage-Grouse

Michael J. Wisdom, Cara W. Meinke, Steven T. Knick,
and Michael A. Schroeder

Abstract. Geographic ranges of Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*C. minimus*) have contracted across large areas in response to habitat loss and detrimental land uses. However, quantitative analyses of the environmental factors most closely associated with range contraction have been lacking, results of which could be highly relevant to conservation planning. Consequently, we analyzed differences in 22 environmental variables between areas of former range (extirpated range), and areas still occupied by the two species (occupied range). Fifteen of the 22 variables, representing a broad spectrum of biotic, abiotic, and anthropogenic conditions, had mean values that were significantly different between extirpated and occupied ranges. Best discrimination between extirpated and occupied ranges, using discriminant function analysis (DFA), was provided by five of these variables: sagebrush area (*Artemisia* spp.); elevation; distance to transmission lines; distance to cellular towers; and land ownership. A DFA model containing these five variables correctly classified >80% of sage-grouse historical locations to extirpated and occupied ranges. We used this model to estimate the similarity between areas of occupied range with areas where extirpation has occurred. Areas currently occupied by sage-grouse,

but with high similarity to extirpated range, may not support persistent populations. Model estimates showed that areas of highest similarity were concentrated in the smallest, disjunct portions of occupied range and along range peripheries. Large areas in the eastern portion of occupied range also had high similarity with extirpated range. By contrast, areas of lowest similarity with extirpated range were concentrated in the largest, most contiguous portions of occupied range that dominate Oregon, Idaho, Nevada, and western Wyoming. Our results have direct relevance to conservation planning. We describe how results can be used to identify strongholds and spatial priorities for effective landscape management of sage-grouse.

Key Words: *Centrocercus minimus*, *Centrocercus urophasianus*, extirpated range, extirpation, Greater Sage-Grouse, Gunnison Sage-Grouse, range contraction, sagebrush.

Factores Asociados a la Extirpación del Sage-Grouse

Resumen. Las distribuciones geográficas del Greater Sage-Grouse (*Centrocercus urophasianus*) y el Gunnison Sage-Grouse (*C. minimus*) se han

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RESULTS

Differences Between Extirpated and Occupied Ranges

Fifteen of the 22 environmental variables had mean values with nonoverlapping 95% CIs between extirpated and occupied ranges (Figs. 18.2–18.4). These variables included five biotic, three abiotic, and seven anthropogenic variables.

The five significant biotic variables were sagebrush area, patch size of sagebrush, proximity of sagebrush patches, size of sagebrush core areas, and distance to the boundary between occupied and extirpated ranges. Historical locations in occupied range contained almost twice as much area in sage-

brush as those in extirpated range (Fig. 18.2). Mean patch size of sagebrush was >9 times larger, and mean core area >11 times larger, in occupied versus extirpated range (Fig. 18.2). Sagebrush patches also were substantially closer to one another in occupied range (Fig. 18.2). In addition, historical locations in occupied range were closer to the boundary between occupied and extirpated ranges than locations in extirpated range (Fig. 18.2).

The three significant abiotic variables were elevation, soil water capacity, and soil salinity. Elevation was almost 50% higher in occupied range than in extirpated range (Fig. 18.3). Occupied range had lower soil water capacity and higher soil salinity (Fig. 18.3).

Biotic Variables

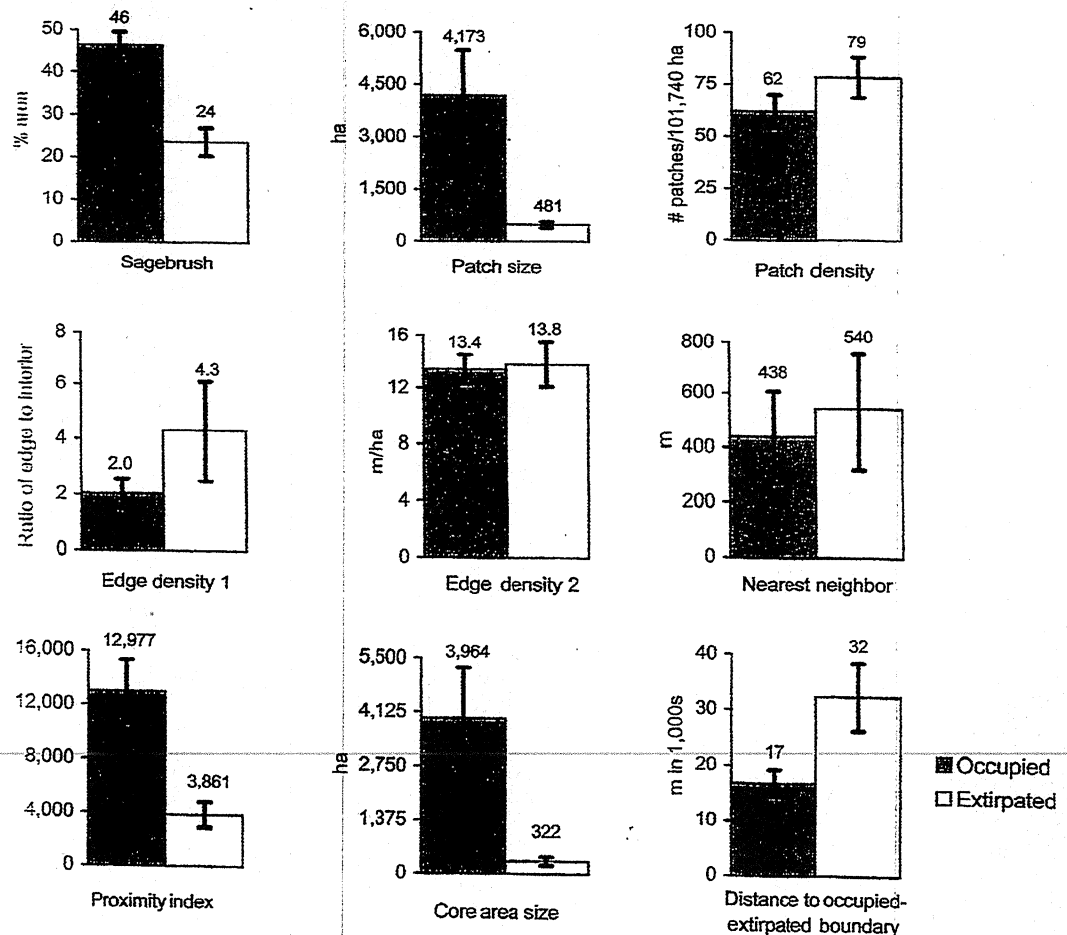


Figure 18.2. Mean values and 95% confidence intervals for nine biotic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

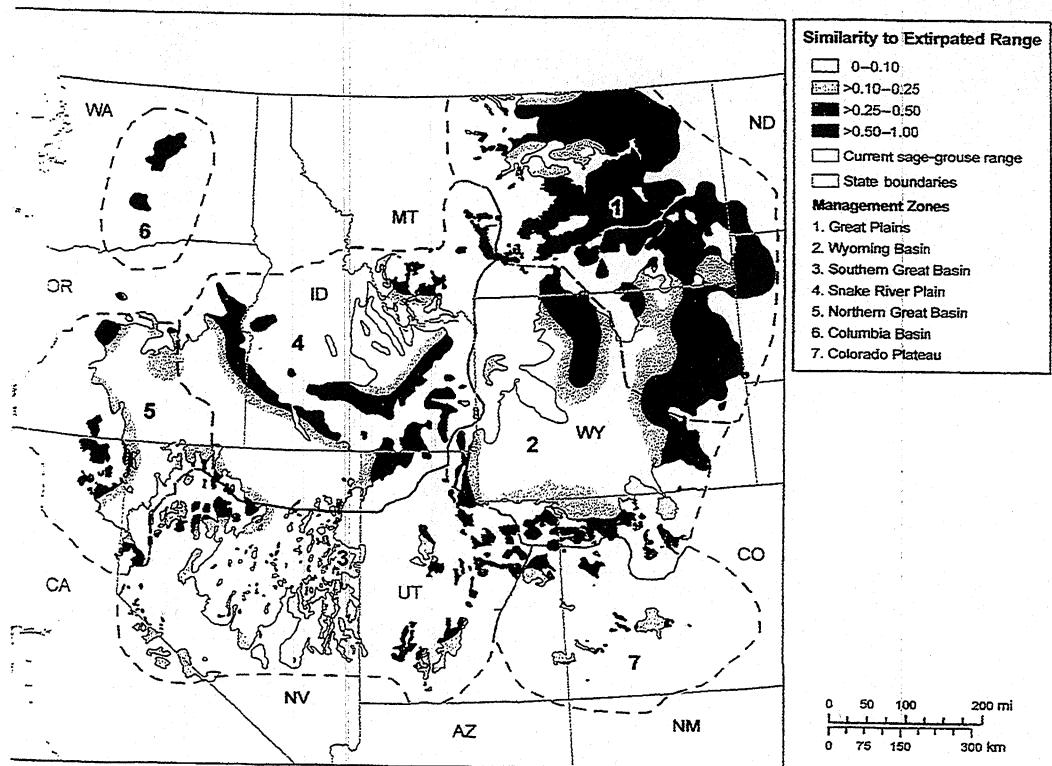


Figure 18.5. Probabilities of environmental similarity of areas currently occupied by sage-grouse with areas where extirpation has occurred, based on estimates from model 2 discriminant function analysis. Probabilities range from 0.0–1.0 and are mapped as a continuous variable. Areas in black show high similarity with extirpated range. Areas in light grey show low similarity.

classes (37%), followed by Colorado Plateau at 10% (Table 18.4). SMZs with lowest similarity to extirpated range were Northern Great Basin, Southern Great Basin, Snake River Plain, and Wyoming Basin. The large majority of occupied range in these four SMZs had probabilities of similarity of ≤ 0.10 . All four, however, had high similarity with extirpated range along range peripheries or in smaller, disjunct areas (Fig. 18.5).

DISCUSSION

Factors Associated with Extirpation

Biotic Variables

Sage-grouse occupation versus extirpation was strongly associated with measures of sagebrush abundance and distribution, including sagebrush area, patch size, proximity of patches, and size of core areas. These results support past studies that identified sage-grouse as a sagebrush obligate,

dependent on sagebrush for persistence (Braun et al. 1976, Schroeder et al. 1999, Rowland 2004).

Sagebrush area was the single best discriminator between occupied and extirpated ranges among the 22 variables evaluated. The DFA model containing this single variable was one of the top-performing models. These results agree with recent findings that sagebrush area is one of the best landscape predictors of sage-grouse persistence (Wisdom et al. 2002c; Walker et al. 2007a, Doherty et al. 2008, Aldridge et al. 2008).

The upper 95% CI for sagebrush area in extirpated range was 27%. Landscapes occupied by sage-grouse with sagebrush <27% would thus have a >97.5% probability of being no different than a random sample of extirpated ranges, suggesting that associated populations in these occupied ranges could be more vulnerable to extirpation. Similarly, the lower 95% CI for sagebrush area in occupied range was 50%. Landscapes occupied by sage-grouse with values above this lower bound thus have a >97.5% probability of being no different than a

random sample of occupied ranges, suggesting a higher capability to support persistent populations.

Recent landscape studies of Greater Sage-Grouse identified similar threshold values for sagebrush area to maintain population persistence. Aldridge et al. (2008:990), using a 30.77-km radius around sampling locations, estimated that at least 25% and preferably 65% of the landscape needed to be dominated by sagebrush for long-term sage-grouse persistence. These estimates mirror our values of 27% and 50% for sagebrush area, with values <27% indicating a high risk of extirpation, and values above 50% indicating a high probability of persistence. Our estimates also are for large landscapes, based on the 18-km radius circles that we analyzed. Similarly, Walker et al. (2007a) estimated that the lowest probability of lek persistence, approximately 40–50%, occurred for landscapes with <30% area in sagebrush within 6.4 km of a lek center. These probabilities declined even more for landscapes with <30% sagebrush that were subjected to energy development (see fig. 5 in Walker et al. 2007a).

Abiotic Variables

Three abiotic variables—elevation, soil salinity, and soil water capacity—also differed between occupied and extirpated ranges. Elevation was a good discriminator, probably because most sagebrush loss has occurred disproportionately at lower elevations where human activities and developments have been concentrated (Hann et al. 1997; Knick et al., this volume, chapter 12; Leu and Hanser, this volume, chapter 13), and where invasive grasses have displaced large areas of sagebrush (Suring et al. 2005b; Meinke et al. 2009). Lower soil salinity and higher soil water capacity in extirpated range also indicate a higher suitability for agricultural development (Knick, this volume, chapter 1), which also was associated with sage-grouse extirpation.

Anthropogenic Variables

Seven of the eight anthropogenic variables differed between occupied and extirpated ranges. The number of these variables, their diversity, and the strength of differences between occupied and extirpated ranges suggest that a variety of human activities and land uses have contributed to or been associated with sage-grouse extirpation. This inference agrees with findings from recent landscape studies that documented negative effects of anthropogenic

variables on sage-grouse populations, including human density and percent agriculture (Aldridge et al. 2008), roads and traffic (Lyon and Anderson 2003, Holloran 2005), and energy development (Holloran 2005; Aldridge et al. 2007; Walker et al. 2007a; Doherty et al. 2008; Naugle et al., this volume, chapter 20). We did not specifically evaluate energy development. However, extirpated range contained almost 27 times the human density, had almost three times more area in agriculture, was 60% closer to highways, and had 25% higher density of roads, in contrast to occupied range. These patterns agree with research cited above that evaluated these or similar variables. Moreover, the four variables of human density, area in agriculture, distance to highways, and road density were part of model 4, which outperformed all models except the top-ranked model 2.

Three additional anthropogenic variables—distance to transmission lines, distance to cellular towers, and landownership—also differed between occupied and extirpated ranges. These variables were the best discriminators among the eight anthropogenic variables considered and ranked among the best of all individual variables. These variables have received little attention in landscape research on sage-grouse—only distance to transmission lines has been formally evaluated (Connelly et al. 2000a, Aldridge and Boyce 2007, Walker et al. 2007a). Transmission lines can cause sage-grouse mortality via bird collisions with lines (Beck et al. 2006, Aldridge and Boyce 2007) and facilitate raptor predation of sage-grouse (Connelly et al. 2000a). In addition, the electromagnetic radiation emitted from transmission lines has a variety of negative effects on other bird species using areas on or near lines (Ferne and Reynolds 2005). Moreover, transmission lines convert habitat to nonhabitat and fragment the remaining habitat, similar to roads (Naugle et al., this volume, chapter 20).

The strong association between distance to cellular towers and sage-grouse extirpation was an especially intriguing result, given that no previous studies of sage-grouse have evaluated this variable. Whether cellular towers function in a cause-effect manner or simply are aligned with other detrimental factors cannot be addressed without additional research. Recent studies, however, suggest possible cause-effect relationships between high levels of electromagnetic radiation within 500 m of cellular towers and reduced population or reproductive performance of a limited