

**Attachment #3 for the Objection filed against the Cooke City
Fuels and Forest Health Project on the Gardiner Ranger
District of the Custer-Gallatin National forest by NEC et al. on
August 18, 2025.**

Attachment #3 contains relevant portions of literature and/or reports cited in the Objection, including:

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*Societal Measures - Protection of trees &
Management produces cones.*

80 yr rot = 62%
300 yr = 90%

*Exotic - Red sp. caused
decline of crossbill in
Newfoundland.*

Logging, Conifers, and the Conservation of Crossbills

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Abstract: A survey of the forestry literature shows that as the age and area of coniferous forests decline, decreased conifer seed production and increased frequencies of cone failures can be expected. This would, in turn, cause declines in crossbills (*Loxia*), which specialize on the seeds held in conifer cones. In western North America, at least five different species of Red Crossbills (*L. curvirostra*) have recently been distinguished (Groth 1990); each specializes on a different species or even a single variety of conifer (Benkman 1993). Measures for conserving this diversity of crossbills include protecting mature and old-growth stands, and increasing rotation ages throughout the range of each of the required conifers. These recommendations are not unique to crossbills, but rather the loss of crossbill diversity is another reason to employ such measures.

Explotación forestal, coníferas y conservación de piquitrueros ("crossbills")

Resumen: Un estudio de la literatura forestal demostró que cuando la edad y el área de los bosques de coníferas declinan, se puede esperar un decrecimiento en la producción de semillas y un incremento en la frecuencia de fracasos de los conos (piñas). Esto, a su vez, puede causar declinación en piquitrueros (*Loxia*), los cuales se especializan en las semillas que se encuentran en los conos de coníferas. En el oeste de Norte América, por los menos cinco especies diferentes de Piquitrueros Rojos (*L. curvirostra*) han sido recientemente identificadas (Groth 1990); cada una está especializada en una especie diferente o incluso en una variedad particular de coníferas (Benkman 1993). Medidas para conservar esta diversidad en piquitrueros incluyen proteger rodales maduros y de crecimiento antiguo e incrementar la edad de rotación a lo largo del rango de cada una de las coníferas requeridas. Estas recomendaciones no son únicas para los piquitrueros, pero la pérdida de la diversidad de los piquitrueros es otra razón para emplear tales medidas.

Introduction

Specialist species are particularly vulnerable to extinction. Among the most specialized groups of birds are the crossbills (*Loxia*), which are adapted for foraging on seeds in conifer cones (Newton 1972; Benkman 1987b, 1988a, 1988b, 1993; Benkman & Lindholm 1991) and whose survival and reproduction depend on the availability of conifer seeds (Newton 1972; Benkman 1987a, 1988a, 1990, 1992a). Crossbills also are a speciose lin-

eage. What had previously been recognized as a single species, the Red Crossbill (*L. curvirostra*) in North America, consists of at least seven distinct species (Groth 1990). Although the taxonomic basis for recognizing these different crossbills at the species level is still largely unpublished (but see Groth 1988), each species differs in morphology, vocalizations, and ecology, and several species commonly nest syntopically without much interbreeding (Groth 1988, 1980; Benkman 1993). Moreover, most if not all of these species of crossbill are adapted specifically for foraging on single species of conifers, and in some cases just one variety of conifer (Benkman 1989, 1993). For instance, in western North America different species of Red Crossbill are

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adapted specifically for foraging on each of western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*), ponderosa pine (*P. ponderosa* var. *scopulorum*), and possibly Sitka spruce (*Picea sitchensis*) (Benkman 1993).

Undisturbed conifer forests were recently widespread but now are among the most intensively exploited habitats (Caufield 1990; McLaren 1990; Norse 1990; also see Rosencranz & Scott 1992). For example, only around 10% of the original old-growth forest in Washington and Oregon may remain (Norse 1990), and most second-growth on federal lands typically has rotation ages of about 80 years (Brown 1985). Many industrial forest lands are managed on a 40 to 60 year rotation (J. F. Franklin, personal communication). Consequently, species dependent on mature conifer forests, such as crossbills, will inevitably decline, with local and possibly global extinctions.

Dependency on a single resource makes crossbills extremely vulnerable to habitat loss and alteration. Because the link between crossbills and their food resources, conifer seeds, is so strong and clear (Newton 1972; Benkman 1987a, 1990, 1992a), the conservation strategy for crossbills is simplified (see Terborgh 1986). Moreover, because the basic mechanisms influencing crossbill ecology are well understood (Newton 1972; Benkman 1987a, 1987b, 1988a, 1989, 1990, 1992a), the general impact on crossbills of habitat alteration, such as that from logging, can be anticipated; this is the subject of this paper. Such predictive analyses are important, in part, because the actual status of nomadic crossbill populations is difficult to assess and large declines may go undetected. For example, during the early 1970s in Newfoundland there appears to have been a severe decline of the formerly abundant and endemic Newfoundland Crossbill (Benkman 1989, 1992b; Pimm 1990). This decline was not noted until nearly twenty years later, however, and only after I had predicted such a result from the introduction (in 1963–1964) of red squirrels (*Tamiasciurus hudsonicus*) onto Newfoundland (Benkman 1989, 1992b). Although I concentrate on crossbills, the impact may be applicable to populations of numerous other conifer seed-eating animals (see Smith & Balda 1979).

Temporal Variation in Habitat Quality

Logging at short rotation ages increases the domination of forests by younger trees (Harris 1984), which, for at least three reasons, greatly reduces cone and seed production relative to mature or old-growth forests. First, shorter rotation ages reduce the proportion of time a given stand is capable of producing seeds (Fig. 1). Most conifers begin producing cones (seeds) only after they

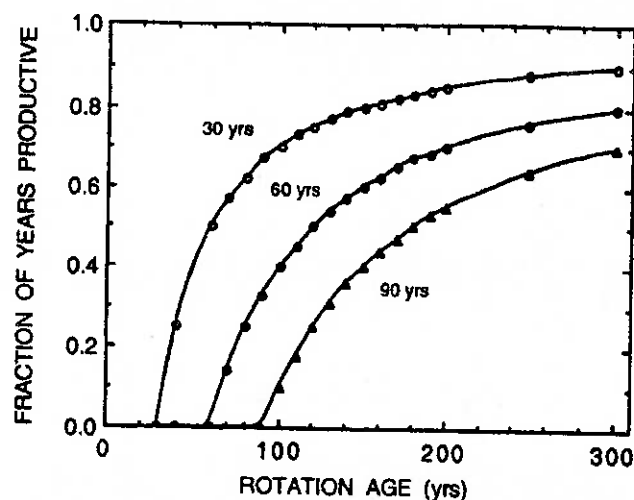


Figure 1. The fraction of years a forest might produce cones in relation to rotation age. The different curves represent different ages (30, 60, and 90 years) after which cones are produced. Although many conifers begin producing cones after 30 years of age (Fowells 1965), the smaller cone crop sizes and the higher frequency of cone failures for younger trees effectively shift the curve down and to the right (toward or below the 90 year curve).

are about 20 to 30 years old (Fowells 1965). Thus, when rotation ages are 80 years and trees produce cones only after 30 years of age, the proportion of time that an area may produce any seed is about five (62%) out of eight years. The intervals between stand-replacing disturbances such as fire or wind in unmanaged stands in western North America are variable, although they usually are greater than 80 years (see Habeck 1988; Peet 1988; Spies & Franklin 1988; Alaback & Juday 1989). For example, west of the Cascade Range many old-growth forests were older than 300 years prior to logging, and many may have been older than 750 years (Spies & Franklin 1988). Assuming that stand-replacing disturbances occur at intervals of 300 years, and that 30 years is the minimum age for cone production, unmanaged stands potentially produce seed at least nine (90%) out of every 10 years. Thus, short rotations increase the proportion of the landscape that is of pre-seed-production age.

Second, younger conifers produce smaller cone crops than do older conifers. For example, an old-growth stand of Douglas fir produces 20 to 30 times more cones than a 50- to 100-year-old second-growth stand (Burns & Honkala 1990). Maximum cone production for some conifers is not reached until trees are 200 years of age (such as the sugar pine [*Pinus lambertiana*; Fowells & Schubert 1956] and Douglas fir [Fowells 1965]). In addition, smaller cone-producing trees in a stand fail to produce cones more often than larger and presumably

older trees (such as ponderosa pine and Douglas fir; Fowells & Schubert 1956, Shearer 1986, Burns & Honkala 1990). This reduces further the proportion of years that harvested forests are productive for seed-eaters. In the above example, a conifer that first begins producing cones at 30 years of age may regularly produce many cones only after 90 or more years of age (see Fig. 1).

Third, seed production by late successional conifers will be especially reduced by short rotations. In the Cascade Range, western hemlock tends to be a major component only late in succession (Franklin 1988) and is, therefore, often only a minor seed producer except in old-growth forests. For example, in the Douglas fir-western hemlock forest type in the Cascade Range of Washington, western hemlock seed production in a 100-year-old stand (mostly Douglas fir) was less than one two-hundredth of that in a nearby old-growth stand (Isaac 1943).

Crossbills are expected to benefit from mature and old-growth forests because they produce many more cones much more consistently over longer periods than do regularly logged forests. Furthermore, the small cone crops of younger forests may act as cone failures for crossbills because they require a minimum seed abundance to survive, with small cone crops less likely to meet minimum energy requirements (Benkman 1987a, 1992a). Moreover, because the larger the cone crop the more crossbills breed (Benkman 1990), the decline in large cone crops should result in smaller rates of increase after cone failures, and hence slower recovery rates.

Spatial Variation in Habitat Productivity

Geographic Variation

Because cone production can vary so much annually within a given area (Fowells 1965), special considerations need to be made to ensure that areas of abundant cones are available every year. Years of good cone production are usually followed by one to several years of little or no cone production; even the most regular cone-producing conifers have occasional cone failures (Fowells 1965). Moreover, large regions often fail to produce many—or any—conifer seeds during one to several years in succession (see Harris 1962), so that crossbills move out of these areas and concentrate where cone crops are produced (see Benkman 1987a). During many years, only a fraction of the total potential range can support crossbills. Thus, a reserve or system of reserves encompassing only a restricted geographic area would be inadequate to support nomadic populations of crossbills continuously, and most crossbill populations are nomadic. Indeed, bird species whose foods irregularly fail in a given area (such as tropical fru-

gives) tend to be "extinction prone" (Terborgh & Winter 1980; also see Janzen 1986).

Climate influences cone crop production and failures (Roeser 1942; Lowry 1966; Lester 1967; Smith & Balda 1979), hence areas experiencing similar climate are more likely to produce cone crops or fail in synchrony (see Kemp & Keith 1970). In western North America, the mountainous terrain affects local climate so that cone crop production is more likely to vary locally (Bock & Lepthien 1976; Smith & Balda 1979). Nevertheless, cone crops can fail synchronously over large mountainous regions (such as the Cascade Range of Oregon and Washington; Franklin et al. 1974).

The greater the number of distinct climatic regions within a forest reserve, the lower the probability of a complete cone failure. For example, six distinct regions, each with an independent probability of cone failure of one in three years (see, for example, Franklin et al. 1974), have a 0.0014 probability of synchronous cone failure (0.333^6). However, if only three of the regions have mature forest, then the probability of synchronous cone failure increases over 26 times to 0.037 (0.333^3). Compounding this further is that the frequency of small cone crops unable to support crossbills through the winter likely increases in younger stands. If as a result of logging the frequency of failure and of small cone crops doubles, the probability that six distinct regions are synchronously unable to support crossbills increases by over 62 times from 0.0014 to 0.088 (0.666^6). The decrease in distinct regions with mature forest and the decline in forest age from logging both compound the probability of synchronous and widespread cone failures, which are pernicious to crossbills (see Newton 1972 and Benkman 1988a for the effect of cone failures on crossbills).

Local Variation

Even within a given region, only certain areas may be favorable enough to maintain crossbills over many years (source habitat, for example, [Pulliam 1988]). Areas that consistently produce large cone crops and hold seeds for extended periods most likely represent source habitat for crossbills. Large cone crops result in high intake rates for crossbills (Benkman 1987a, 1987b), which improves their reproductive rates (Benkman 1990) and presumably their survival (Benkman 1987a). The value of reserves in protecting crossbills, therefore, depends critically on the amount of productive land or source habitat protected.

Unfortunately, for the same reasons habitats are most productive for crossbills (edaphic characteristics and climate favorable for cone production) they are likely to be most productive for commercial interests and to be intensively managed. In the Pacific Northwest, for example, lowland forests are the most productive, and

they have been largely logged (Norse 1990). Most of the remaining old growth in the Pacific Northwest is at higher elevations on steep slopes (Norse 1990). Here, cane production is less than at lower elevations because it often declines with increases in elevation (as in Douglas fir and ponderosa pine [Jacobsen 1986]). In fact, most protected areas (such as wilderness areas) are confined to higher elevations (Harris 1984), where conifers likely produce fewer seeds than at lower elevations where logging is permitted.

Habitat Fragmentation

As remnant forest patches become smaller and more isolated and fragmented, many forest species decline disproportionately relative to forest loss (Wilcove et al. 1986). Crossbills have been found to decline as forests are fragmented (Helle 1985). However, their decline is more likely in response to the concurrent decline in forest age as a result of logging rather than to habitat fragmentation per se (Helle & Järvinen 1986). Forest fragmentation is likely not as detrimental for crossbills, which regularly may fly distances for greater than 1 km (Benkman, personal observation), as it is for other old-growth species (Norse 1990). Thus, local management policies that account for more area-sensitive species (such as the Northern Spotted Owl *Strix occidentalis caurina* and Northern Goshawk [*Accipiter gentilis*]) would be adequate for crossbills.

Habitat fragmentation, nevertheless, may make crossbills more vulnerable to extinction by reducing the rate at which suitable patches of habitat (those containing a good cone crop)—are colonized. Levins (1969, 1970) has shown that when extinction rates of local individual populations exceed colonization rates, the species or metapopulation may go extinct. Crossbills can be thought of as being composed of many populations repeatedly colonizing patches of habitat containing good cone crops, and then going extinct locally when the cone crop fails. As patches become smaller and more isolated, their rate of colonization by crossbills may decline. Because a nomadic crossbill may need to colonize many patches during its lifetime, even slight declines in colonization rates can be important.

Evidence of Adverse Effects on Crossbills

As expected from much greater seed production in old than young forests, Red Crossbills were more abundant in older than in younger forests in Finland (Helle & Järvinen 1986) and in northern California (Raphael et al. 1988). In another study, Red Crossbills were 30 times more abundant in old-growth (325 to >500 years old) than in younger (65 to 140 years old) forests during two years of poor seed crops in the Cascade Range of south-

ern Washington (Huff et al. 1991). Such a pronounced difference occurred because the only conifer to produce seeds was the late-seral (at least in this forest type) western hemlock, and it was of cone-producing size and age only in the old-growth forests (Manual & Huff 1987; Huff et al. 1991; see previous discussion).

Although this system has not been modeled, diminished cone production and the increased isolation of productive habitats as a result of logging will likely result in declines of crossbills even within mature forests (see Fahrig 1992). Consequently, crossbill abundance should decline disproportionately to forest loss. Evidence of declines in crossbills that are disproportionate to the loss of habitat has been found in northern Finland: as the proportion of land containing older forests (>121 years old) diminished by 27% between the early 1950s and 1970s because of clear-cutting, Red Crossbills declined by 75% (Väisänen et al. 1986). Väisänen et al. (1986) also present evidence that crossbills declined even within an unaltered forest.

In sum, older forests tend to support more crossbills than do younger forests, and as the proportion of the landscape containing older forests declines, crossbills decrease disproportionately in abundance. This could have been anticipated from our knowledge of the natural history of crossbills and of conifer seed production. We should anticipate that if the extent and frequency of logging increases, crossbills will continue to decline and will become increasingly vulnerable to environmental and demographic stochasticity and to losses to genetic variability (see Lande 1988).

Conclusions and Recommendations

Protecting nomadic populations of crossbills presents some of the same challenges confronted in the conservation of migratory species (Myers et al. 1987), where species often concentrate in small areas during their annual cycle. However, protecting nomadic species such as crossbills represents a more formidable challenge because critical habitats are more difficult to recognize since they may be used only once every several years, with different areas crucial during different years. Nonetheless, several practices would aid crossbills and other conifer seed-eating animals.

First, as a general rule, the amount of old-growth forest should be maximized simply because it is consistently the most productive for crossbills. In areas where little old growth remains (such as Siuslaw National Forest in coastal Oregon [Harris 1984]), second-growth should be protected and allowed to mature. Especially beneficial to the crossbills specialized on Douglas fir and western hemlock is the recent proposal to protect an additional 2.4 million ha of U.S. Forest Service and Bureau of Land Management lands in northern California,

western Oregon, and western Washington to protect the Northern Spotted Owl (Thomas et al. 1990).

Second, rotation ages of managed forests need to be lengthened. In western North America, the proportion of lands logged and the rotation ages set by the U.S. Forest Service and Bureau of Land Management will have a profound impact on crossbill populations, because these two agencies control most of the federal forests required by crossbills (see Crumpacker et al. 1988). A similar arrangement exists in Canada, where even less old-growth forest is protected from logging than in the United States (for example, only about 17,600 ha of old-growth Sitka spruce-western hemlock forest were protected in British Columbia as of 1987 [Roemer et al. 1988; see also Beebe 1991]).

Third, mature trees should be left in cutover areas (as in partial cuts; see Franklin & Spies 1991). This will act to increase the proportion of the landscape containing trees of cone-bearing age. Furthermore, the remaining trees, released from competition, may then produce larger cone crops (see Fowells 1965). However, because cross-pollination and the number of full seeds per cone declines as mature tree density decreases (Smith et al. 1988), there will be a lower limit to tree density below which crossbills cannot be supported in the long term.

Fourth, because geographically separated areas often produce cone crops asynchronously, a geographically limited reserve of each forest type, (such as spruce-hemlock forest) will be inadequate for protecting nomadic populations of crossbills. Forest reserves should be located among as many distinct climatological regions as possible to avoid synchronous cone failures among all areas, and to minimize the risk from catastrophes (see, for example, Walters 1991). Tree seed zones, each of which represent different climates and elevations, represent such distinct regions (Schopmeyer 1974). Information on geographic variation (morphological or phenological) in conifers can also be used in determining favorable distributions of forests, because morphological variation is correlated with climate (such as ponderosa pine [Fowells 1965] and Douglas fir [Sorensen & Miles 1978]). The policy to protect forest tracts throughout the Northern Spotted Owl's range (Thomas et al. 1990) will reduce the likelihood of a complete cone failure in the Pacific Northwest.

Fifth, reserves should encompass productive forests. This will be difficult where commercial interests are powerful. For example, in the Cascade Range the most productive areas are low-lying valleys, of which few are protected (Norse 1990).

Last, aiding seed-eating animals will seem heretical to silviculturalists, who have invested a considerable amount of energy eradicating these animals (see Fowells 1965). However, by increasing rotation intervals, we enhance seed production and especially the occurrence

of large cone crops. Because the greatest fraction and by far the greatest number of seeds remain uneaten during large cone crops (see Fowells & Schubert 1956), they are the most critical for natural regeneration. By increasing rotation ages (and the amount of old growth) we can increase the occurrence and extent of large cone crops and thereby protect the great diversity of conifer seed-eating animals (see Smith & Balda 1979).

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NESTING AND FORAGING HABITAT OF GREAT GRAY OWLS

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ABSTRACT.—During 1982–1986, 46 Great Gray Owl (*Strix nebulosa*) nests were located in northeastern Oregon. Twenty-five of these nests were on stick platforms, 11 were on artificial platforms, and 10 were on broken-topped dead trees. Mean dbh and height of trees containing stick nests were 58 cm and 30 m, respectively, and the majority (76%) of nests were in live western larch (*Larix occidentalis*). Broken-topped dead trees with nests averaged 78 cm dbh and 11 m tall. Forest types in which nests were found included: Douglas-fir (*Pseudotsuga menziesii*)–grand fir (*Abies grandis*) (50%); western larch–lodgepole pine (*Pinus contorta*) (29%); ponderosa pine (*Pinus ponderosa*)–Douglas-fir (15%); and ponderosa pine (7%). Nesting males foraged primarily in mature, open stands (11–59% canopy closure) of ponderosa pine or Douglas-fir.

The Great Gray Owl (*Strix nebulosa*) is the largest strigiform found in North America and is an impressive owl of great interest to bird enthusiasts. This circumpolar species is widespread and occurs in boreal forests from Alaska, east to Ontario, south to Idaho, western Montana, northwestern Wyoming, northern Utah, northern Minnesota, northern Wisconsin, and the Sierra Nevada in California; in Eurasia, this owl occurs in northern portions of Scandinavia, Russia and Siberia (American Ornithologists' Union 1983).

Surprisingly little is known about the Great Gray Owl, making management difficult. To manage for the species, information on the habitat used for nesting and foraging is essential. If foraging habitat is lacking and prey densities are low, the owls will not nest even if nest sites are available. If prey is adequate and nest sites are lacking, again there will be no nesting.

Because these owls depend on existing nest platforms such as old raptor nests, broken-topped dead trees, and artificial platforms (Nero 1980; Mikkola 1983; Winter 1986; Bull et al. 1987; Franklin 1987; Forsman and Bryan 1987), managers have a good opportunity to manage the species by providing nest platforms where they want the owls—provided there is adequate prey and habitat to support them. It is therefore essential to know what habitats are suitable for nesting and foraging.

Our objectives were to determine habitat used for nesting and foraging of Great Gray Owls during the breeding season in northeastern Oregon. Nesting habitat included the nest tree and the area surrounding the tree, in addition to the habitat used by ju-

veniles after fledging who were still dependent on the adults. Foraging habitat included areas used by males who were feeding females and offspring.

STUDY AREA

During March–May 1982 we surveyed for Great Gray Owls in 2 large areas: the area within a 60-km radius around La Grande, Oregon and a 50 km² area 47 km north of Enterprise, Oregon. During 1983–1986 survey efforts were confined to 4 areas where Great Gray Owls were located in 1982—the Spring, Bowman, Sheep and Thomason study areas.

Forest types in each area were categorized using a modification of Burr's (1960) classification by tree species in the dominant and codominant crown classes. Dominant trees were defined as those with crowns extending above the general level of the crown, and codominant trees were those whose crowns formed the general level of the crown (Smith 1962:33). Each of the 4 study areas contained 4 different forest types: 1) ponderosa pine (*Pinus ponderosa*), 2) ponderosa pine–Douglas-fir (*Pseudotsuga menziesii*), 3) Douglas-fir–grand fir (*Abies grandis*), and 4) western larch (*Larix occidentalis*)–lodgepole pine (*Pinus contorta*).

Successional stages in each area were classified based on tree size and stand structure as subclimax, mature, over-mature and remnant. In subclimax stands all trees were <30 cm dbh; in mature stands the largest trees were 30–50 cm dbh; over-mature stands were unlogged and larger trees were ≥50 cm dbh; remnant stands were typically logged and had 1–3 trees/ha ≥50 cm with the remainder of trees <30 cm. The remnant stage identified stands that did not resemble unlogged over-mature stands but contained a few large-diameter trees.

The Spring study area (44 km²) was 17 km west of La Grande at 930–1140 m elevation. Cover types included conifer forest (63% of area), shallow-soiled grasslands (32%) and clearcuts (5%). During the previous 10 yrs, 66% of forested stands within the Spring study area had been selectively logged. As a result most forests in this area consisted of open, park-like stands dominated by ponderosa pine. These stands were on deep soils with a dense cover of grasses. Isolated stands of unlogged, large trees (≥50 cm dbh) comprising 22% of this study area remained. Isolated stands contained Douglas-fir, lodgepole pine,

¹ Deceased.

110- one study area
had 141 ac/ pair
- another = 320 ac/ pair

Table 1. Characteristics of 3 types of Great Gray Owl nest structures at 46 nest sites in northeastern Oregon, 1982-1986.

CHARACTERISTIC	NEST STRUCTURE					
	STICK	BROKEN-TOPPED TREE		WOODEN PLATFORM		
No. nests in Spring	16	1		4		
No. nests in Bowman	3	2		2		
No. nests in Sheep	5	1		—		
No. nests in Thomason	1	6		5		
Nest tree species						
Western larch	76%	10%		45%		
Douglas-fir	20%	20%		—		
Ponderosa pine	4%	70%		36%		
Lodgepole pine	—	—		18%		
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
Nest height (m)	17	5.05	11	3.88	12	3.01
Tree dbh (cm)	58	17.16	78	15.24	58	17.20
Tree height (m)	30	4.98	11	3.65	29	8.73
Bole height (m)	10	5.00	8	4.24	13	6.59
Tree age	151	35.07	173	25.40	129	51.73

78 cm =
= 30.7"

western larch, and occasionally grand fir. A total of 52 artificial nest platforms were erected in 1984 in the Spring area.

Bowman (27 km²) was 50 km west of La Grande at 1380-1500 m elevation. Cover types included coniferous forest (68%), shallow-soiled grasslands (20%) and clearcuts (12%). Dense stands of lodgepole pine or mature and over-mature stands of grand fir and Douglas-fir with some western larch and ponderosa pine dominated the Bowman area. About 60% of the forested area had been logged in the 15 yrs prior to our study; lodgepole pine stands had been clearcut, and ponderosa pine and Douglas-fir stands had been selectively logged. Fifty-four artificial nest platforms were erected in this area in 1984.

Sheep (78 km²) was 37 km southwest of La Grande at 1290-1500 m elevation. Cover types included coniferous forest (68%), clearcuts (12%), wet meadows along streams (12%) and shallow-soiled grasslands on ridges (8%). Ponderosa pine forests occurred on south-facing slopes, and lodgepole pine stands or mixed stands of Douglas-fir, western larch and grand fir occurred on north-facing slopes. Greater than 80% of the forested area had been logged (40% clearcut and 60% selectively logged) during the 15 yrs prior to this study.

Thomason (34 km²) was 47 km north of Enterprise at 1350-1470 m elevation. Cover types included coniferous forest (71%) and wet meadows (29%). Forest stands were lodgepole pine and ponderosa pine or mixed stands of Douglas-fir, western larch and grand fir. About 80% of the area had been selectively logged in the 10 yrs prior to this study. There were 38 artificial nest platforms in Thomason at the onset of this study.

METHODS

Locating Birds and Nests. Owls were located after dark in February, March and April by imitating the territorial call of a male Great Gray Owl every 0.1 km while walking through each study area. Areas containing owls were searched for active nests during the day.

Radio Telemetry. Adult Great Gray Owls were captured with bal-chatri traps, noose poles and mist nets (Bull 1987). Radio transmitters (AVM Instrument Co.—SM1, L Module) were placed on 10 males and 13 females and 35 post-fledging juveniles. Transmitters were attached to the bird with a back-pack harness of 6 mm tubular teflon ribbon. The entire package weighed 25 g and lasted 242-505 d. A Telonics TR-2 receiver with a hand-held 2-element Yagi antenna was used for locating owls.

Adult radio-tagged owls were located each spring at their nests. Juveniles were located every 1-3 d for 7 d after fledging. Eight nesting males were followed in the morning (first light until roosting) and evening (departure from roost until dark) 1-2 times/wk from the time transmitters were put on until 2 mo after fledging, or until the radio failed or the nest was abandoned.

Habitat Quantification. Variables recorded at nests included nest type (stick, broken-topped dead tree, or artificial platform), nest height (m), tree species, dbh (cm), height (m), age (increment bore used), and bole height (height of lowest live branch) (m) (Table 1). Stick nests were classified as natural platforms created by dwarf mistletoe (*Arceuthobium* spp.) or as vacated nests built by Northern Goshawks (*Accipiter gentilis*) or Red-tailed Hawks (*Buteo jamaicensis*). At 4 sites we saw hawks con-

Surveys,

Table 2. Habitat characteristics in circular 0.1-ha plots centered on 46 Great Gray Owl nests in north-eastern Oregon, 1982-1986.

CHARACTERISTIC	$\bar{x}$	S.D.	FRE- QUENCY
Forest type			
Douglas-fir-grand fir			50
Lodgepole pine-western larch			29
Ponderosa pine-Douglas-fir			15
Ponderosa pine			7
Successional stage			
Mature			26
Over-mature			41
Remnant			33
Logging			
None			72
Partial cut			19
Adjacent to clearcut			9
Canopy closure (%)			
0-10			7
11-59			30
≥ 60			63
Live trees/0.1 ha ≥ 50 cm dbh	3.2	2.51	
Dead trees/0.1 ha ≥ 50 cm dbh	1.0	2.10	
Live trees/0.1 ha < 50 cm dbh	26.7	14.70	
Dead trees/0.1 ha < 50 cm dbh	9.2	7.80	
Leaning trees/0.1 ha < 10 cm dbh	5.1	14.45	
Regeneration (trees/0.1 ha)	41.8	55.47	
Distance to water (m)	231.6	209.98	
Distance to clearing (m)	77.1	70.13	

structing nests in prior years; at the remainder, a nest below the canopy in a dense forested stand was classified as an old Goshawk nest, and a nest high in the canopy of a more open forest was classified as an old Red-tailed Hawk nest.

In a circular 0.1-ha plot centered on each nest, we recorded the variables listed in Table 2. Regeneration included all trees ≤ 10 cm dbh. We also recorded landform (flat, draw, or slope), slope aspect and gradient, number of canopy layers and height (m) of tallest canopy. With aerial photos (scale 1:24 000) and a planimeter, we determined the percent area in forest, grassland, clearcut and selectively logged forest within a 500-m radius of each nest. The linear distance in edge between forest and grassland within the 500-m radius was calculated with a map measure. Edge was defined as a 60-m wide band where forests and openings met.

Juvenile owls were located every 1-3 d during the week after fledging. Each time a juvenile owl was located, we recorded type of perch used (branch, leaning tree, or top

of a broken-off dead tree) and perch height. Tree species, condition (live or dead), dbh, and height of the tree used for perching were measured. In addition we noted the presence of leaning trees that provided owlets access to perches in upright trees. For the next 2 mo, juveniles were located every 1-2 wks and locations recorded on aerial photographs.

While following radio-tagged males, activity and habitat use data were recorded at 15-min intervals and each time an owl hit the ground when pursuing prey (hereafter referred to as a foraging site). Activity categories were hunting or roosting. Birds actively searching for prey, flying from perch to perch, and staring intently at the ground were classified as hunting. Birds quietly perched in a tree next to the trunk and not watching the ground intently were classified as roosting.

Every 15 min we recorded location of the bird on an aerial photo, estimated canopy closure over the bird and recorded forest type, successional stage, physiognomy of the stand (open or dense forest or edge), logging activity, number of stand layers, type of perch and tree species supporting perch. If a bird was roosting when first located, we recorded the data once and waited until the bird left the roost before continuing.

At each foraging site we recorded percent, height and type of ground cover within a 1-m radius, presence or absence of downed wood within a 1-m radius, diameter (at largest point) of the downed wood, distance owl flew to prey, height of perch, diameter of perch tree and distance to nest. Home range of hunting males was delineated by connecting the outermost radio locations to form minimum convex polygons which were then measured with a planimeter.

LANDSAT data (Isaacson et al. 1982) were used to determine forest canopy closure classes (0-10%, 11-59% and $\geq 60\%$) available in 3 of the study areas and in the home range of 5 of the 8 males. The 0-10% class comprised openings; the 11-59% class contained relatively open stands, many of which had been selectively logged; the $\geq 60\%$ class was primarily unlogged, overmature forest stands.

Density. We calculated density of active nests of Great Gray Owls in Spring and Thomason by counting the number of nests within a polygon defined by the outermost nests in 1984. We chose 1984 because we believe all nesting pairs within the polygons were located that year. We did not present the density as number of nests/study area because we believe all nests in the study areas were not found.

Analysis. Chi-square analyses were used to compare the observed number of foraging locations in each canopy closure class and in edge with the expected number of locations based on the percent edge and canopy closure classes in the home range of each radio-tagged male. We compared habitat characteristics of hunting birds in Spring with those in Bowman and Sheep using a Chi-square analysis. Habitat used by 3 birds studied in Sheep and Bowman were combined because of the small sample size and because the 2 areas had similar habitat and logging activity. We used $P < 0.05$ as the level of significance. We could not test for preference for nest type or nest habitat because we did not determine the number or distribution of available nest sites.

RESULTS

Nest Sites. During 1982–1986, we located 46 nests, 14 of which were used more than once (Table 1). Of the 14 nests used more than once, 6 were used 2 years, 6 were used 3 years, 1 was used 4 years, and 1 was used twice in the same year, so we observed 69 nesting attempts on 46 nest structures. Fifty-four percent of the nests were stick platforms, 24% were artificial platforms and 22% were natural depressions on broken-topped dead trees (Table 1). Of the stick nests, 68% were originally made by Northern Goshawks, 12% were made by Red-tailed Hawks and 20% were natural platforms created by dwarf mistletoe infections.

All 3 types of nests were commonly used, although nests in broken-topped trees and wooden platforms had a lower rate of nest failure (20%) than did nests in stick platforms (34%), suggesting that the latter was a less stable structure because young or eggs fell through on at least 4 occasions. The majority of stick nests were in large diameter (≥ 50 cm dbh) live western larch (Table 1). The majority of nests in broken-topped dead trees were in large diameter ponderosa pine at least 7 m tall. Nests in wooden platforms were at least 9 m above the ground in live trees.

The mean size of 11 stick nests was 74 cm (SD = 17.32) long, 65 cm (S.D. = 11.97) wide, 27 cm (S.D. = 14.04) high, with a depression 7 cm (S.D. = 2.70) deep. The only nest on a broken-topped dead tree that was measured had a circular depression in the top of the tree that was 56 cm in diameter and was 26 cm deep.

The majority of the nests occurred in Douglas-fir–grand fir forest types and in over-mature and remnant stands (Table 2). Sixty-nine percent of nests occurred on slopes, 22% on flat ground, and 9% in draws; mean slope gradient at nests was 13% (S.D. = 9.28). Sixty-five percent of nests were on north-facing slopes. Northern aspects are preferred by Northern Goshawks (Reynolds et al. 1982), the primary builder of nests used by Great Gray Owls.

Western larch comprised the dominant crown class at 52% of nest sites, ponderosa pine 28%, and Douglas-fir and grand fir the remainder. Ponderosa pine comprised the dominant crown class at nests in Thomason, and western larch comprised the dominant crown class in the other study areas. The co-dominant crown class was comprised of lodgepole pine at 51% of the nests, Douglas-fir at 31% and ponderosa pine at 18%.

Seventy-two percent of nest sites had not been logged, but 60–80% of stands in each study area had been logged. Forty-four (96%) of 46 nest sites had ≥ 2 canopy layers, the tallest layer having a mean height of 34 m (S.D. = 4.90). Density of live trees < 50 cm dbh at nest sites ranged from 5–64 stems/0.1 ha, and of live trees ≥ 50 cm dbh ranged from 0–10 stems/0.1 ha. Density of dead trees ranged from 0–36 stems/0.1 ha at nest sites. Regeneration ranged from 0–290 stems/0.1 ha.

Area in forest within a 500-m radius of each nest ranged from 52–99%, and forested area that had been logged ranged from 0–97%. The amount of edge between forests and openings within 500 m of the nest averaged 4.2 km (range = 0.7–8.3 km). The amount of area in natural openings within 500 m of the nest ranged from 0–40%. Nests in Thomason contained the greatest amount of natural opening ($\bar{x}$ = 25%), and nests in the other 3 study areas contained 13–15%. Bowman contained the greatest amount of clearcut area (13%) within 500 m of nests; nests in the other 3 areas contained $\leq 6\%$. Total area in openings (natural and clearcut combined) ranged from 18–26%.

Nest Site Fidelity. We observed 18 nesting attempts by 9 pairs where at least 1 member of each pair was radio-tagged. Of the 18 nesting attempts, 39% were on the same nest the next year, 39% were within 1 km of the nest used the previous year, and 22% were farther than 1 km away from the nest used the previous year. Average distance between alternate nests was 1.3 km (range = 0.2–4.5 km, Fig. 1). In 4 cases in which a bird or a pair moved farther than 1 km from their previous year's nest, we found previous nest sites occupied by new pairs.

Density. Shortest distance between 2 active nests was 430 m; 2 other nests were 460 m apart. In 1984 the minimum density of owls was 7 pairs/9.4 km² (entire study area was 44 km²) at Spring and was 5 pairs/2.9 km² (entire study area was 34 km²) at Thomason. At Spring, 2 different females used the same nest in 1984 and were counted as 2 pairs.

Perches Used by Juveniles. Owlets left the nest before they could fly but were capable climbers, using talons, bills and wings to claw and flap their way up tree trunks. For the first few days, leaning trees with bark were easiest for the young to climb. After several days, juveniles could climb up some vertical trees, particularly those with branches or deeply fissured bark (characteristic of large-diameter trees). As owlets aged, they perched higher in the

$$\begin{aligned} 5 \text{ pr} / 2.9 \text{ km}^2 \\ = 1.0 \text{ owl} / .58 \text{ km}^2 \\ = .22 \text{ sq mi} \\ = 141 \text{ acres} \end{aligned}$$

$$\begin{aligned} 7 \text{ pr} / 9.4 \text{ km}^2 &= 1.3 \text{ km}^2 / \text{pr} \\ &= 0.5 \text{ sq mi or } 320 \text{ acres} \\ \text{Shortest distance nests} &= .22 \text{ mi} \end{aligned}$$

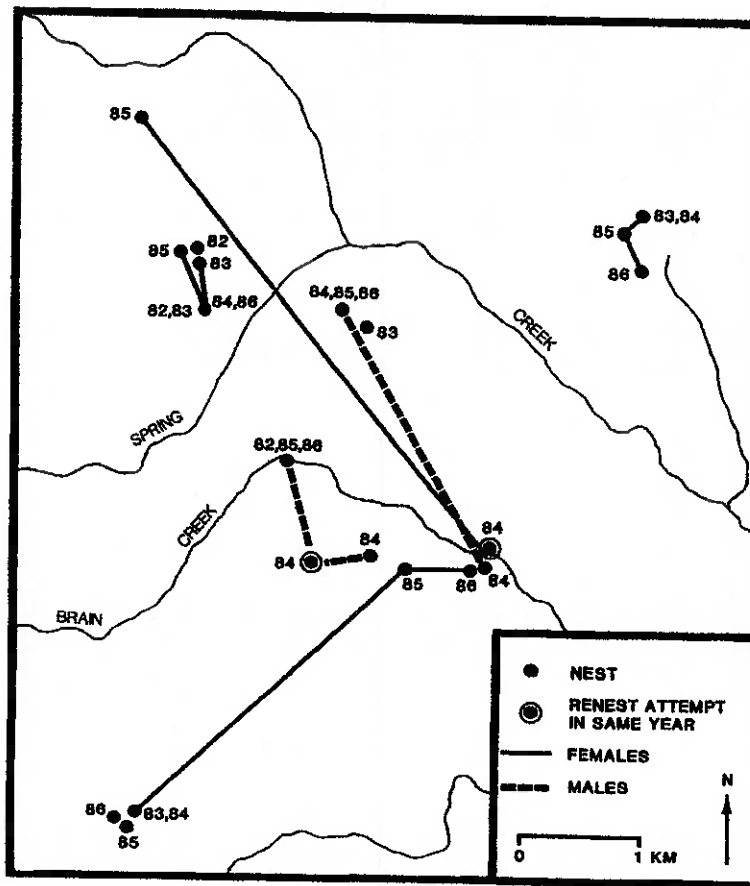


Figure 1. Locations of nests of radio-tagged Great Gray Owls in Spring area 1982-1986. Lines connect nests used in successive years by the same bird.

canopy. Perches used the first week after the young left the nest averaged 6.2 m (S.D. = 4.13) above the ground, had an average canopy closure of 50% (S.D. = 22.16) and were all within 200 m of the nest.

Of 116 perches used by juveniles, 67% were leaning trees or trees which could be reached by climbing a leaning tree; the remainder were branches or broken-topped trees. Leaning perch trees were typically small-diameter ($\bar{x}$ = 16 cm, S.D. = 7.82) lodgepole or ponderosa pine, with an average of 87% (S.D. = 23.80) of the bark remaining. Branches used as perches were typically in live ponderosa pine or Douglas-fir trees with a mean dbh of 37 cm (S.D. = 20.10).

After leaving the nest, juveniles typically moved toward dense forest cover (if the nest was not in a

dense stand). Within 2 wks after fledging juveniles gradually became more mobile but generally stayed within forest stands with $\geq 60\%$ canopy closure (Fig. 2). Family group C ranged the farthest and roosted less frequently in stands with dense canopies than did other family groups (Fig. 2).

Foraging Habitat. During 229 hrs of radio-tracking 8 male Great Gray Owls, we recorded 223 foraging sites and 622 hunting locations at 15-min intervals. Males usually hunted in open forested stands from perches close to the ground. Hunting perches averaged 5.5 m (S.D. = 6.65) high and were in trees with mean dbh of 27 cm (S.D. = 14.06). Mean distance males flew from perches to prey was 10.5 m (S.D. = 9.39). Vegetative ground cover at foraging sites averaged 88% with an average plant

perches =
close to
ground
18'

67%
perches
leaning
tree.

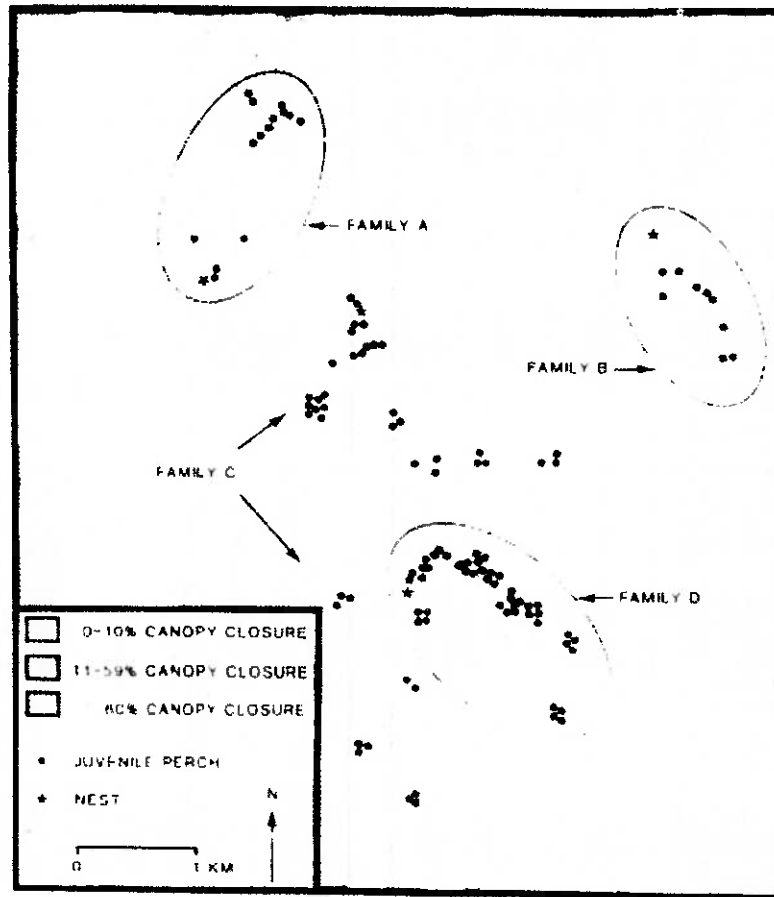


Figure 2. Location of nests and perches used by juveniles of 4 Great Gray Owl family groups in Spring study area. Juveniles were located during 2 mo after fledging. Family groups A and B nested in 1983, and family groups C and D nested in 1985.

height of 21 cm. Grasses dominated in 96% of the sites. Downed wood with a mean diameter of 20 cm was present within 1 m in 77% of the sites.

Mean distance the 8 males moved from the nest when hunting was 0.62 km. One male foraged no further than 0.7 km from his nest, whereas the greatest distance foraged by a male was 3.2 km. Home range of 5 males with ≥ 90 foraging locations averaged 4.5 km² (range = 1.3–6.5 km²).

There was a significant difference in canopy closure of stands used for foraging by 5 males compared to expected use based on availability (χ^2 values for 5 males: 48.1, 41.1, 37.3, 109.8, 58.4; 2 df, $P < 0.01$). Males preferentially foraged in stands with

11–59% canopy closure and avoided clearings. Four of the males avoided stands with $>60\%$ canopy closure, while 1 male used such stands in proportion to their occurrence. Use of edge was significantly greater ($P < 0.05$) than expected with 2 males, less than expected with 2 males, and not different than expected with 1 male.

There were significant differences between 5 foraging males at Spring and 3 at Sheep and Bowman in all habitat variables measured except canopy closure (Table 3). Males at Spring hunted more often in stands that were open, logged, younger, with 1–2 canopy layers and containing more ponderosa pine than did males at Sheep and Bowman (Fig. 3). Males

$$\text{Home Range} = 1.3 \rightarrow 6.5 \text{ km}^2 =$$

$$= 0.5 \text{ m}^2 (320 \text{ ac}) \rightarrow 2.5 \text{ m}^2 (1600 \text{ ac})$$

$$\text{Area used while nesting} = \text{avg}$$

at Sheep and Bowman hunted more often in stands that were unlogged, older, with 2-3 canopy layers and containing more Douglas-fir and lodgepole pine.

Males roosted during the day in stands with 11-59% canopy closure (71%) and stands with 60% or more canopy closure (29%). Eighty-three percent of 62 roost sites were in mature or older stands with 2 or more canopy layers. Sixty-eight percent of roosts were in unlogged stands. Owls roosted at least 7 m above the ground 56% of the time, 3-6 m above the ground 38% of the time and lower than 3 m 6% of the time.

DISCUSSION

Great Gray Owls are versatile in their use of nest structures and readily use artificial nests. In Finland Mikkola (1981) observed the species using nests on branches, on stumps, on the ground, on a cliff and on a barn. Great Gray Owl use of artificial nest structures has been reported by Nero et al. (1974), Nero (1982) and Helo (1984) and provides opportunities for management. Owls may prefer artificial structures over natural platforms; 3 females in our study nested on platforms even though stick nests were available nearby.

Great Gray Owls are flexible in their use of habitats as well. Nero (1980) and Servos (1986) found Great Gray Owl nests in poplar (*Populus* spp.) and tamarack (*Larix laricina*) trees adjacent to muskeg in Canada. Winter (1986) found nests on dead trees in conifer forests only within 260 m of meadows in California. Harris (1984) described nests in forests of tamarack and black spruce (*Picea mariana*) in Canada, and Mikkola (1981) reported nests in dense spruce and pine forests, deciduous stands, wet spruce moors, and swamps in Finland and Sweden. Mikkola (1981) suggested that the owls preferred edges of older stands rather than the interior of large, dense forests. In Oregon we found Great Gray Owl nests in all forest types available within the study areas; however, the majority of nests were in over-mature or remnant stands of Douglas-fir and grand fir forest types on north-facing slopes.

Although the majority of each study area had been logged within 15 yrs of our study, 72% of nests occurred in unlogged stands. Either owls preferred unlogged stands or there was a disproportionate number of potential nest sites in stands, as logging activities often remove large-diameter live and dead trees that could support nests.

Leaning trees and dense cover near nests are im-

Table 3. Foraging site characteristics of 8 nesting male Great Gray Owls in northeastern Oregon, 1985 (data in percent).

CHARACTERISTIC	SHEEP/ SPRING BOWMAN ^a	
	(N = 357)	(N = 265)
Forest type ($\chi^2 = 264.2$, 3 df, $P < 0.01$)		
Ponderosa pine	62	3
Ponderosa pine-Douglas-fir	25	5
Douglas-fir-grand fir	11	60
Lodgepole pine-western larch	2	32
Successional stage ($\chi^2 = 12.1$, 3 df, $P < 0.01$)		
Subclimax	23	17
Mature	61	58
Over-mature	6	6
Remnant	10	19
Physiognomy of stand ($\chi^2 = 82.6$, 2 df, $P < 0.01$)		
Open forest	84	51
Edge	14	30
Dense forest	2	19
Logging ($\chi^2 = 54.2$, 2 df, $P < 0.01$)		
Unlogged	25	49
Partial cut	74	46
Clearcut	1	5
No. stand layers ($\chi^2 = 130.6$, 2 df, $P < 0.01$)		
1	46	13
2	52	54
3	2	33
Perch location ($\chi^2 = 28.3$, 2 df, $P < 0.01$)		
Branch	68	55
Trunk	27	25
Leaning tree	5	20
Tree species of perch ($\chi^2 = 318.2$, 3 df, $P < 0.01$)		
Ponderosa pine	82	7
Lodgepole pine	9	55
Douglas-fir	7	25
Other	2	13

^a The 3 birds in Sheep and Bowman were combined due to sample size.

portant habitat components for fledglings. Owlets left the nest before being able to fly, but leaning trees enabled owlets to climb to perches above the ground. Without leaning trees owlets would be vulnerable to terrestrial predators.

Male Great Gray Owls foraged in a variety of habitats; partially logged stands did not appear to be detrimental, as 62% of foraging locations occurred

Preferred
habitat

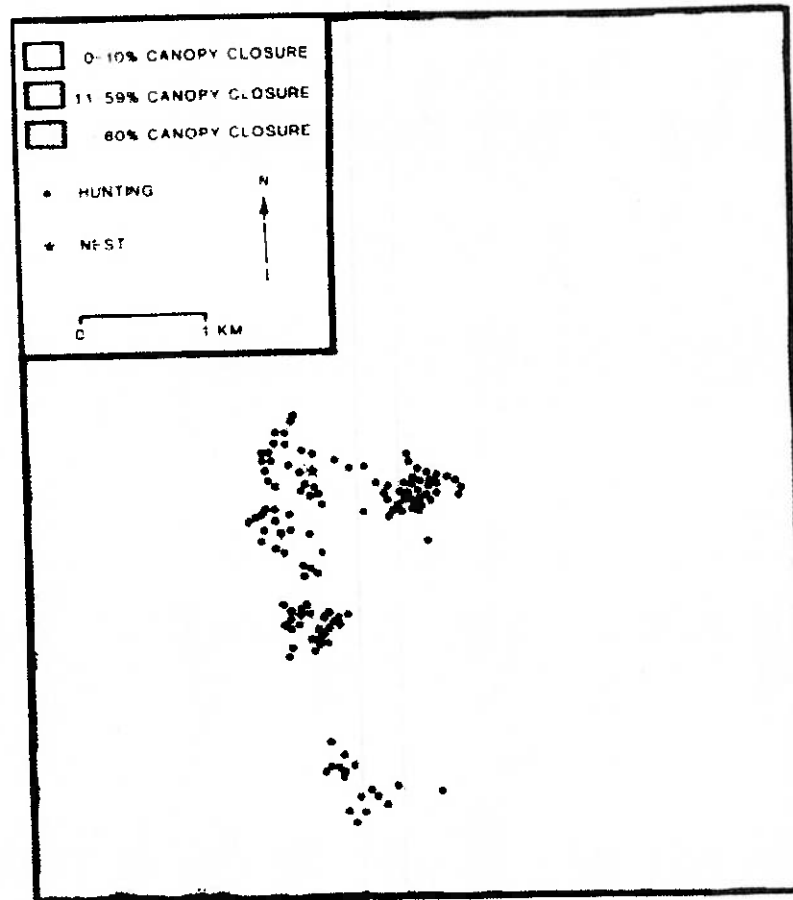


Figure 3. Locations at 15-min intervals of a hunting male Great Gray Owl in Spring study area during daylight. Observations were made on 10 d from 1 April–22 July 1985.

there. Open stands of mature forests were used most for foraging, while subclimax and dense over-mature stands and clearcuts were used less frequently. Winter (1986) reported that Great Gray Owls foraged primarily in or along meadow edges; Franklin (1987) found them foraging in clearcuts. Factors that are important in foraging habitats include high prey density, perch availability and forests that are open enough to allow birds to move freely.

Relatively close spacing of some nesting pairs in Oregon support the belief that Great Gray Owls defend only the immediate vicinity around a nest (Bull and Henjum 1987). Höglund and Langren (1968) reported pairs within 100 m of each other in

Sweden; Mikkola (1976) reported 3 nests within 400 m of each other in Finland; and Wahlstedt (1974) reported 5 pairs within 3 km in April. More recently, Lehtoranta (1986) found 2 nests in Finland only 49 m apart, but since only 1 male was seen, polygamy seems possible.

Because the species does not generally maintain mutually exclusive territories, fairly high densities can be obtained. Mikkola (1981) reported 8 nests in 100 km² in Finland, and Wahlstedt (1974) found 5 nests and an additional 4 pairs that he believed were nesting in a 100 km² area in Sweden. In Oregon we found the highest density of nesting Great Gray Owls reported for either North America or Europe.

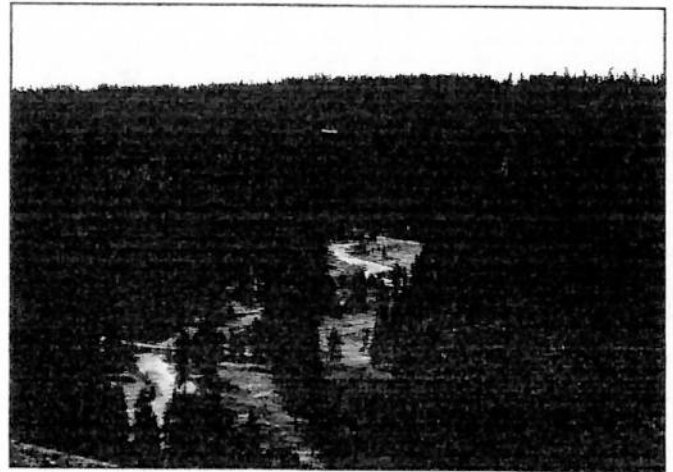
Trees and Logs Important to Wildlife in the Interior Columbia River Basin

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INTRODUCTION



More than 80 species of birds, mammals, reptiles, and amphibians use living trees with decay, trees with brooms, hollow trees, snags, and logs in the interior Columbia River basin. Animals use these structures for foraging, nesting, denning, roosting, and resting. Most notable of these wood-using wildlife species are the primary cavity nesters, the woodpeckers and nuthatches, that excavate nest cavities in decayed wood in standing trees. Their vacated cavities are subsequently used by many other birds and mammals. About 25 percent of the bird species nesting in the northern Rocky Mountain forests are cavity nesters (McClelland and others 1979). Many of the primary and secondary cavity-nesting birds eat forest insects and thus play an important role in regulating their populations. Machmer and Steeger (1995) provide a thorough review of the effect these birds have in reducing numbers of tree-feeding insects.

Tree decay is an important ecological process affecting wildlife habitat. Once begun, the decay process can take hundreds of years as a tree dies, falls to the ground, and decomposes into the forest floor. As it decays, the tree supports many different wildlife groups that use it for foraging substrate, for nesting, and for shelter. The group of wood decomposers is diverse. It includes many arthropods, but in this publication, we focus on decay fungi as the primary organisms in decay. Decay fungi are an essential resource to forest ecosystems in storing and retaining nutrients and in soil development.

This publication provides managers with a description of the ecological processes that create wildlife trees, snags, and logs. It provides qualitative and quantitative information on five distinct structures: living trees with decay (such as internal decay), hollow trees, trees with brooms (misshapen branches), dead trees (snags), and down woody material (logs). We describe the value of these structures to wildlife, the decay or infection processes that produce each type of structure, principles to help in selecting the best structures to retain, and management implications. Although this document cannot prescribe the amount of landscape to manage

for a particular species or a specific, desired population size, it does present information managers can use to make informed decisions regarding the conservation and enhancement of dead wood structures most valuable to wildlife. Forest management practices that fail to properly manage wood components may adversely affect wildlife, soil and stream quality, and forest ecosystem functions.

The information included here applies to coniferous forest lands in the interior Columbia River basin: the area east of the crest of the Cascade Range in Oregon and Washington, all of Idaho, and a portion of western Montana (fig. 1). Tree species characteristic of high-elevation forests, (such as whitebark pine [*Pinus albicaulis*], alpine larch [*Larix lyallii*], mountain hemlock [*Tsuga mertensiana*], and Pacific silver fir [*Abies amabilis*]) are excluded because they typically grow where active management for wildlife trees is seldom needed; these areas are seldom logged. Most of the tree species we deal with here are conifers, although black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) are

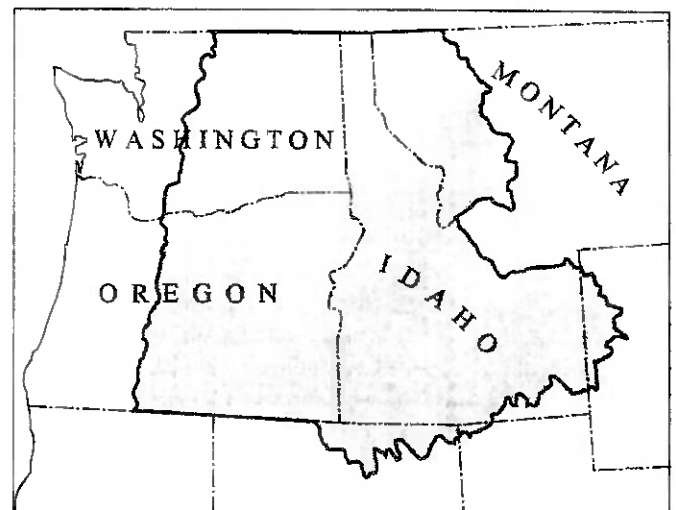


Figure 1—The interior Columbia River basin.

Snag distribution—Snags can either be left in clusters or scattered across the landscape, although where to retain them depends largely on where they currently are. Typically, snags are in clumps naturally because the agents of disease, insects, fire, or flooding that kill many trees act in a localized area. Clusters of snags may be easier to protect during management activities than snags evenly distributed across the landscape. Worker safety is an issue when harvesting adjacent to snags. Retaining snags in clusters, as well as the live trees between the snags, keeps workers away from snags and provides canopy cover for wildlife using the snags.

Two studies on woodpecker use of snag clusters reported different results. No difference was found between woodpecker use of snag clusters versus scattered snags in western Oregon (Chambers 1997). In areas where stand-replacement fires had burned in ponderosa pine/Douglas-fir stands in Idaho, Saab and Dudley (1997) found that cavity nesters as a group select clusters of snags for nest sites instead of evenly spaced trees.

5-2
Most studies recommend managing snags in every 5- to 25-acre patch (Bate 1995, Evans and Martens 1995). Because woodpeckers are territorial, only one pair of each species occupies the same territory; therefore, to attain the maximum density of cavity nesters, snags need to be distributed across the landscape.

In addition, retaining snags on all aspects and on all positions of the slope ensures habitat availability for wildlife species with different preferences. For example, pileated woodpeckers tend to roost in draws during summer but roost higher on slopes in winter (Bull and others 1992). Martens rest or travel in riparian areas a third of the time in summer but only half that often in winter; upper slopes are used half the time in winter but only a third of the time in summer (Bull 1995).

Retaining snags close to living trees provides cover for cavity users. If snags are retained in the middle of a clearcut, species like northern flickers, Lewis' woodpeckers, bluebirds, and American kestrels (*Falco sparverius*) will use them for nesting, but most other woodpeckers will not nest in open areas.

AP
In many areas, fuel-wood cutters are likely to remove snags along roads. This potential problem can be remedied by not leaving snags in areas that are accessible to fuel-wood cutters or by not counting snags left adjacent to accessible roads toward the number retained for a particular stand.

In summary, wherever the objective is to provide viable populations of primary and secondary cavity nesters, prudent managers will provide large-diameter snags when available, snags in a variety of structural classes, snags in every 5- to 25-acre stand and in clusters if available, and snags on all slope aspects and positions of the slope, and adjacent to green trees.

Snag densities—Limited information is available on numbers of snags to retain for wildlife species in the interior Columbia River basin (Bate 1995, Bull and Holthausen 1993, Dixon 1995, Evans and Martens 1995) (table 1). The guide most widely used in the past, Thomas and others (1979), prescribed the number of nest and roost trees to leave for specified woodpecker populations, but the number was based on a hypothetical, untested model and did not include any snags for foraging. Three studies (Bate 1995, Bull and

Holthausen 1993, Dixon 1995) conducted in eastern Oregon have shown that retaining foraging structure is essential, in addition to nest and roost trees in managed landscapes. The Thomas model provided only two roost trees per pair per year, yet research has shown that individual pairs of pileated woodpeckers and white-headed woodpeckers use considerably more than two per year (Bull and others 1992, Dixon 1995). Radio-telemetry studies have shown that home range sizes of pileated woodpeckers (Bull and Holthausen 1993), white-headed woodpeckers (Dixon 1995), and three-toed and black-backed woodpeckers (Goggans and others 1988) are considerably larger than those used in the Thomas model. Raphael and White (1984) found that the relation between numbers of snags and cavity nesters is not linear, which was assumed in the Thomas model. The substitution factor used in the Thomas model is variable and largely a function of snag density. Neitro and others (1985) thought allowing substitution of snags that reduced the number retained was not appropriate. The Thomas model did not take into account the habitat needs of some of the secondary cavity nesters, like bats and brown creepers, that use such snag features as loose bark. In addition, Bull and Holthausen (1993) found lower densities of pileated woodpeckers in nine study areas than predicted by Thomas and others (1979) based on the number of snags present. The above studies present new data suggesting that some of the assumptions and data used in the Thomas model are not valid, and that the prescribed snag densities need to be revised upward.

We know of only three studies in the interior Columbia River basin that have calculated both the density of snags and woodpeckers in managed and unmanaged landscapes. Bate (1995) used six study areas in ponderosa pine stands and found woodpecker abundance was best predicted by hard snag density, large green tree density, canopy height, and number of canopy layers. Of the nine study areas, only one represented a relatively unmanaged forest with the number of snags that probably approximated historical ones. In this stand, Bate found 3.8 snags greater than 10 inches d.b.h., and 60 percent were larger than 20 inches d.b.h. These snag numbers supported 32.3 woodpeckers per 247 acres and represented the study area that most likely supported viable populations of cavity nesters. Dixon (1995) found similar results in some of the same study areas Bate used.

Another study relating woodpecker density to snag density was conducted in northeastern Oregon (Bull and Holthausen 1993). The two study areas that contained viable populations of pileated woodpeckers had an average of 4.2 and 3.8 snags (10 inches or larger d.b.h.) per acre and 0.5 and 0.4 nesting pairs per 247 acres, respectively. The two study areas were in lightly managed landscapes predominated by mixed-coniferous stands with a high density of logs.

Evans and Martens (1995) recommended densities of snags for retention on the Payette National Forest based on their ecological value, encompassing soil health, seedling regeneration, moisture retention, nutrient recycling, and wildlife use (table 1). The numbers that they recommended were derived from actual snag numbers identified during

timber inventory and vegetation plots but were scaled down to the lower ranges of the snag numbers for the recommendations and include snags 10 inches d.b.h. and larger.

Ideally, data would be available on the exact number of snags required to support specific populations of primary and secondary cavity nesters. Unfortunately, this kind of information is not available. We do know, however, that the snag numbers presented by Thomas and others (1979) are not adequate to support the populations intended because of a lack of foraging strata and invalid assumptions used in the model. If management agencies have an objective to manage for viable populations of woodpeckers, providing numbers of snags that have been shown to support viable populations in the recent studies would be prudent.

Although snags are the key structure typically focused on for cavity nesters, realizing the importance of the forest surrounding the snags also is essential. Some species like the pileated and white-headed woodpeckers and American martens are associated with older forests. For white-headed woodpeckers, the snags must be in association with large-diameter ponderosa pines. For pileated woodpeckers and martens, logs, large-diameter green trees, and a dense canopy are needed. Leaving large-diameter snags or green trees in younger forests, also has value as providing biological legacies.

Snag retention in burns—The above management implications apply to healthy green stands. With vast areas of Oregon, Washington, and Idaho burned by wildfires in the 1990s, there is much interest in determining numbers of snags to retain in burned areas after harvesting. Saab and Dudley (1997) reported that woodpeckers selected nest sites with snag densities greater than those measured at random sites in ponderosa pine/Douglas-fir forests with stand-replacing fires. From 10 to 14 snags per acre were retained in burned stands that were harvested; about 38 to 42 snags per acre were in the unharvested burned stands. Seven species of cavity nesters using the burned stands selected nest sites with more than 20 snags per acre, where snags were distributed in clumps. Lewis' and white-headed woodpeckers, and American kestrels selected the largest, most heavily decayed snags available for nesting. Evans and Martens (1995) presented recommendations for numbers of snags to leave in burned stands.

Green tree replacements—Snags are a dynamic resource; old snags fall and living trees die to become new snags. Snag-dependent wildlife need a continuous supply of snags over time. To provide a continuum of snag habitat, future snags must be planned for by leaving green trees to eventually become snags in managed stands. To determine the number of green tree replacements, information on fall rate of standing snags, snag density, live stem density, and mortality rate of live stems is required. Various models have been developed to calculate the number of green trees to provide for recruitment when specific stand inventory information is available (Bull and others 1980, Cimon 1983, Schommer and others 1993). If snags are to be created by killing green trees when the stand becomes snag deficient, the number of green trees required is less because the manager does not have to rely on natural mortality to replace

those snags that fall. Creating snags is costly, however, and stands are seldom monitored to determine when trees need to be killed.

Snag Longevity

Snag longevity, or the amount of time a snag stands, is essential information for managing the snag resource. The length of time snags stand is a primary factor in determining the number of green tree replacements needed to maintain a specific snag density over time. Snag longevity is a function of many factors including species, diameter and height, percentage of heartwood, cause of death, soil type and moisture, forest type, and prevalence of windstorms. Because so many factors influence how long a snag stands, fall rates should be determined by species and size class on each management area. Listed below are studies that report snag fall rates. When possible, the amount of time when 50 percent of snags in a particular study have fallen will be reported.

Several studies have reported fall rates of beetle-killed ponderosa pine. Keen (1955) reported that 50 percent of the ponderosa pines in southern Oregon and northeastern California fell 9 to 10 years after death on pumice soils and 6 to 7 years after death on loam soils. The percentages of snags that fell after 7 years by diameter class, are presented in the following tabulation:

Diameter class (inches)	Percentage
10-18	75
20-28	65
30-38	50
40-48	35
> 50	30

Most of the beetle-killed ponderosa pines in Colorado fall between 7 and 10 years after infestation (Schmid and others 1985). Trees were 7 to 22 inches d.b.h.

In northeastern Oregon, half the ponderosa pines less than 10 inches d.b.h. fell 7 to 8 years after death and half those 10 to 19 inches d.b.h. fell after 8 to 9 years (Bull 1983). Beetle-killed lodgepole pines have similar fall rates, with half of those less than 10 inches d.b.h. falling within 6 to 7 years and half of those 10 inches and larger falling after 7 to 8 years (Bull 1983). In a second study in northeastern Oregon (Bull and Partridge 1986), half of the ponderosa pine snags less than 20 inches d.b.h. fell after 6 years; half of the ponderosa pine snags 20 inches and larger fell after 9 years.

Beetle-killed spruce in Colorado stood much longer than ponderosa pines reported in the studies above. Mielke (1950) found that 84 percent of beetle-killed spruce remain standing after 25 years. Hinds and others (1965) found that 72 percent of beetle-killed spruce remain standing after 20 years.

Fire-killed snags may or may not stand longer than beetle-killed snags, depending on the area. Dahms (1949) reported that a little over half the ponderosa pine snags are down 10 years after a fire in central Oregon. In Montana, nearly half of all lodgepole pine snags fall by the fifth season (Lyon 1977). In California, Kimmey (1955) described the

breakup of a fire-killed stand, although specific fall rates were not presented. In the fourth and fifth year after the fire, many ponderosa and Jeffrey pine (*Pinus jeffreyi*) broke off at the ground or up to 50 feet above the ground. By the fifth year, the general breakup continued until only scattered barkless snags and stubs remain.

In northeastern Oregon, different methods of killing ponderosa pines were investigated (Bull 1996c, Bull and Partridge 1986). Trees that had been topped stand the longest; half of those less than 20 inches d.b.h. are down after 10 to 12 years; half of those 20 inches or larger are down after 12 to 17 years. Half the trees injected with a silvicide are down 7 years after treatment. Half the girdled trees are down 9 years after treatment.

Fall rates of snags that have been created differ. Ponderosa pines infected with dwarf mistletoe were frilled and poisoned with an herbicide in the Southwest; after 10 years, 95 percent of those trees are down (Fairweather 1995).

All of these studies suggest that most ponderosa pine and lodgepole pine that died from fire or beetles in the interior Columbia River basin have fall rates of less than 10 years. Small-diameter snags fall sooner than do larger ones.

Sampling Techniques

Knowledge of snag density is essential for managing forest stands effectively, as well as for complying with standards and guidelines. Various methods have been used to determine snag densities: area-wide counts, fixed-radius circular plots, variable-radius plots using prisms (Bull and others 1990), and variable-strip transects (Bate and others, in press). Total counts of snags over large areas are very time-consuming but yield the most accurate density information. Fixed-radius plots typically need to be at least 1 acre because snags are usually scarce and variance is high. Many plots are usually required to accurately estimate snag density.

Bate and others (in preparation) have developed a more efficient method of sampling snags than either area-wide counts or fixed-radius plots: data are collected from a pilot sample transect and used in a computer program. The program determines the optimal length and width of a strip transect within a given area; the optimal size is that which minimizes the cost and variance. The program then provides the necessary sample size to obtain a snag density within the desired statistical bounds. Transect lengths are either 164 or 328 feet; transect widths range from 33 to 131 feet. The

Table 1—Density of snags reported or recommended in four areas; numbers are snags per acre larger than 10 inches d.b.h. (unless otherwise stated), and the percentages represent snags larger than 20 inches d.b.h.

Forest type	Locality			
	Western Idaho ^a	Central Oregon ^b	Northeast Oregon ^c	North-central Idaho ^d
Ponderosa pine:				
Open canopy ^e	1.6(75%)			
Closed canopy ^f	4.8(44%)	4(60%)		
Mixed conifer:				
Open canopy	2.5(72%)			
Closed canopy	9.0(39%)		3.8(29%)	10-48
Lodgepole pine:				
Open canopy	4.5			
Closed canopy	7.7			
Spruce/fir	9.5(21%)			

^a Recommendations for snag densities selected from the lower ranges of snag numbers on timber inventory plots and fixed-radius plots on the Payette National Forest; different snag levels recommended for burned and unburned stands (Evans and Martens 1995).

^b Snag numbers based on variable-width transects conducted in an unmanaged stand of old growth in central Oregon where woodcutting was prohibited (Bate 1995).

^c Numbers based on density of snags in two 4,000-acre study areas in northeastern Oregon that supported viable numbers of pileated woodpeckers; areas had some timber harvest but no woodcutting (Bull and Holthausen 1993).

^d Densities based on timber inventory plots in unmanaged stands of large saw timber. The snag density varied depending on what snags were included in the count. The 10 snags per acre included only snags 15 inches d.b.h. or larger and 50 feet or taller. The 48 snags per acre included all snags 15 inches d.b.h. or larger of any height. Western white pine snags were not counted (Craig 1995).

^e Stands with less than 30 percent canopy closure.

^f Stands with more than 30 percent canopy closure.

program also provides a "distribution index," which is an estimate of the percentage of the sampled landscape supporting target snags or trees.

Creating Wildlife Trees

In managed stands, retaining existing snags is the most ecologically sound and economical approach to providing wildlife trees. If stands are devoid of snags, however, an option is to alter or kill living trees. Depending on the method used, killing trees can be costly and may not produce the desired decay conditions. Years may pass before the decay is sufficiently advanced to promote cavity-nester excavations.

Bull and Partridge (1986) investigated six methods of killing ponderosa pine. They determined that topping trees with either a chainsaw or explosives produced snags that stood the longest and received the greatest nest use by woodpeckers (figs. 48 and 49). In this study, girdling, fungal inoculation, and beetles attracted by pheromones did not consistently kill the tree. Trees killed by girdling or silvicides fell over too quickly to provide wildlife nest trees.

In a study in New Mexico, all of the ponderosa pines killed by girdling were used for foraging by woodpeckers. Most of the trees greater than 16 inches d.b.h. were standing after 7 years, and about 30 percent contained woodpecker nest sites (Parks 1996b). Because the climate in the New Mexico sites is drier than in the Oregon study area used by Bull and Partridge (1986), basal decay of killed trees may have been less, so the trees stood longer.

Recent work by Parks and others (1996a, 1996b) documents a new method of inoculating live trees with decay fungi. Six years after inoculation of 60 living western larch, 14 percent contained woodpecker cavities near the point of inoculation. These trees may remain alive for decades with a pocket of decay that woodpeckers can use for nesting. Trees may be logged next to these trees without safety concerns, and live trees are less likely than dead trees to be lost to fuel-wood cutters. These preliminary results for western larch suggest that inoculation produces desirable wildlife trees at a lesser cost than killing trees to create snags.

A variety of wildlife tree structures can be created with a chainsaw in standing, living trees. Trees can be topped leaving a horizontal branch structure on which ospreys (*Pandion haliaetus*) can build nests (fig. 50). A depression can be cut into the top of a tree that has been topped to produce a nest site for great gray owls (fig. 51). Artificial cavities and hollows can be cut into standing and downed trees (figs. 52, 53, and 54). Slits can be cut into trees to create roosting habitat for bats (fig. 55). These techniques and others are described by Brown (1996).

Three primary considerations in creating wildlife trees are the target wildlife species for which the structure is being created; the tree species, size of tree, and habitat locality most likely to be used by the targeted wildlife species; and the method of altering or killing trees that is most likely to produce long-standing trees in a given geographic area. Rainfall, snowfall, incidence of windstorms, and prevalent decay organisms all must be considered.

Thousands of trees have been killed to create snags in the interior Columbia River basin in the last 15 years. Few of them have been monitored, however, to determine whether long-lasting, quality snags were actually produced. Because climate and decay organisms differ with area, results of management activities, such as snag creation, must be monitored to ensure that results warrant the cost of these treatments. We include a data form to monitor wildlife use of created snags in appendix A.

Review

- Ponderosa pine, western larch, quaking aspen, and paper birch are favored tree species for nest sites of woodpeckers in many areas in the interior Columbia River basin.
- Large-diameter snags provide nest habitat for the greatest variety of cavity nesters and stand longer than smaller snags.
- Snags can be classed into three structural classes that are a simplified version of past decay class categories.
- Snags should be provided in every 5- to 25-acre stand, in clusters if available, on all slope aspects and positions of the slope, and adjacent to green trees.
- Recent studies have shown that the snag model developed by Thomas and others (1979) did not accurately predict woodpecker abundance based on snag abundance. New information suggests that foraging strata (snags and other structures) must be incorporated into any snag model, and that snag numbers need to be revised upward.
- Published data suggest that populations of cavity nesters were viable in stands of ponderosa pine and mixed-conifer forests that contained about four snags per acre, a large component of old-growth stands, and abundant logs.
- Snags can be retained over time by using models for green tree replacements.
- Snag longevity depends on cause of death, tree species, diameter, height, amount of heartwood, geographic area, and site conditions.
- Creating snags and other wildlife structures can mitigate the loss of natural habitat, but retaining existing structures is most cost effective and ecologically sound.

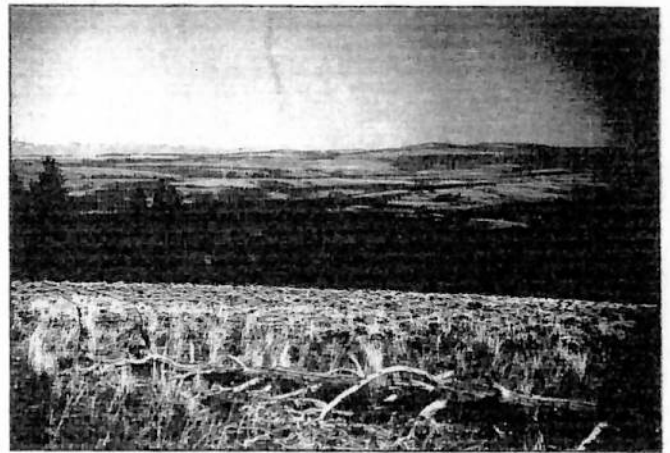


Review

- Size, species, and number of logs per acre are fundamental descriptors of the suitability of log resources for wildlife.
- Logs 15 inches or greater in large-end diameter are particularly important for species such as pileated woodpeckers.
- In mixed-conifer stands, logs of western larch, Douglas-fir, and grand fir were favored for foraging by pileated woodpeckers in northeastern Oregon.
- Late- and old-seral stands of mixed conifers have about 90 logs per acre in northeastern Oregon.
- Logs averaged 34 feet long in mixed-conifer stands in northeastern Oregon, but logs should be as long as possible to offer the greatest range in diameters.
- Hollow logs of any species and size class are important structural components to favor.



CONCLUSIONS



Thomas
This document presents new information on the retention and selection of trees and logs most valuable to wildlife. This new information may be useful in the forest planning process. As additional information becomes available, agencies can incorporate it into their management guidelines.

Current direction for providing wildlife habitat on public forest lands does not reflect this new information. Since the publication of Thomas and others (1979), new research suggests that to fully meet the needs of wildlife, additional snags and habitat are required for foraging, denning, nesting, and roosting. Although we do not suggest specific numbers of snags to retain by forest type, two recent studies indicate that viable woodpecker populations occurred in areas with about four snags per acre (Bull and Holthausen 1993, Dixon 1995).

We suggest that the next step in snag management should involve creating a model that incorporates the new information on woodpecker foraging substrates (live trees, snags, and logs), home range sizes, number and characteristics of roost trees, multiple occupancy of snags, and needs for other habitat structures. Once this information is incorporated, the model may suggest changes to guidelines that specify numbers of snags and other habitat features by forest type and geographic area. Additional information on fall rates of snags, foraging needs of black-backed and three-toed woodpeckers, relation of the density of woodpeckers to that of secondary cavity nesters, and relation of snag density to woodpecker density would greatly improve the model.

A
Although hollow trees provide benefits to many wildlife species, no framework regarding their management exists. Additional research is needed to clarify how and when heart-rot decay is initiated, and how long hollow trees persist. Management actions that foster the development and retention of hollow trees need to be developed.

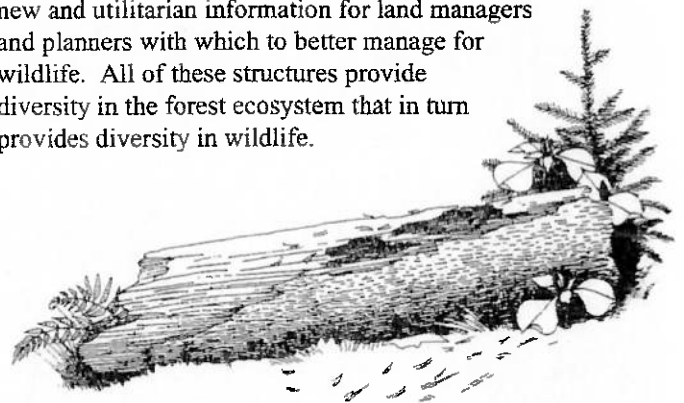
In spite of the value of dwarf mistletoe brooms to wildlife, many managers are still reluctant to retain such structures in stands. With creative management, selected areas can be identified in which to retain trees with dwarf mistletoe brooms but still minimize the risk of spread of

dwarf mistletoe to the rest of the stand. Information presented here suggests that retaining trees with brooms caused by broom rusts or *Elytroderma* offers little risk of tree mortality within a stand.

We are just beginning to recognize the importance of logs in wildlife management. Inventories in 22 areas in northeastern Oregon showed that late- and old-seral stands of mixed conifers contained about 90 logs per acre. These inventories raise questions regarding current guidelines that call for only 6 to 20 logs per acre. Logs are important not just for wildlife but for maintenance of nutrient recycling, water economy, and structural properties for plant growth and soil development that logs provide.

For any management plan to be effective, a reasonable estimate of existing conditions is essential. To obtain this information, inventories of snags, logs, hollow trees, and trees with brooms can be done by using techniques recommended in this text. For down logs, the minimum information needed for wildlife purposes are large-end diameters of logs, lengths, and numbers per acre. Fuel inventories do not provide this information. Once existing conditions are known, management direction can dictate the number and type of structures to retain and the number that can be removed without jeopardizing wildlife objectives.

We hope that this document will provide some new and utilitarian information for land managers and planners with which to better manage for wildlife. All of these structures provide diversity in the forest ecosystem that in turn provides diversity in wildlife.



High elevation
- winds pg 7

RESULTS OF BOREAL OWL (*Aegolius funereus*) SURVEYS ON THE JEFFERSON DIVISION OF THE LEWIS & CLARK NATIONAL FOREST

by

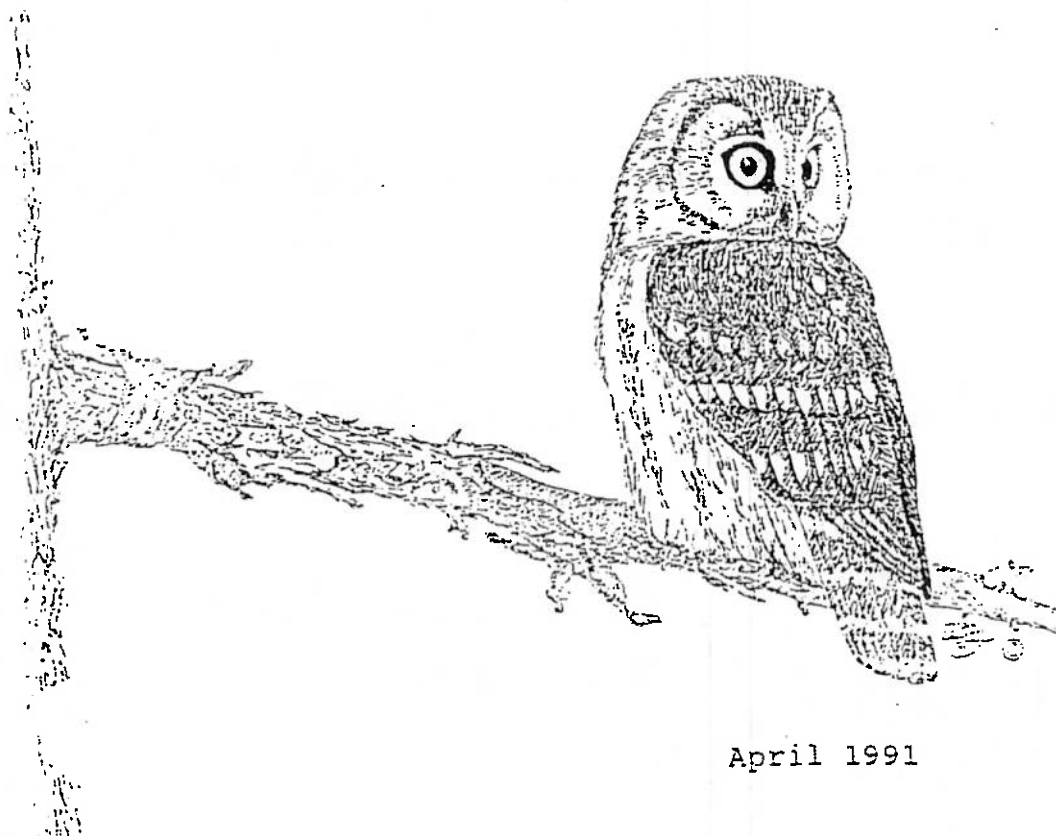
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Cooperative Challenge Cost Share Program
Montana Natural Heritage Program
Lewis and Clark National Forest



April 1991

SUMMARY

A survey for boreal owls was conducted on the Lewis and Clark National Forest in the Little Belt Mountains of central Montana during February and March of 1991. The call playback method was used to survey for owls on 19 nights. A total of 13 survey routes were established, encompassing 87 calling points and 70.2 miles. Some routes were surveyed more than once for a total of 88.5 miles. All owl observations were recorded and mapped. Habitat classifications were obtained from timber typing maps for all boreal owl locations. Boreal owls were heard at 8 calling points, represented 6 individuals. All but one were located in lodgepole pine (*Pinus contorta*) timber types. The other was in a whitebark pine (*Pinus albicaulis*) timber type. All were located between 6400 ft. and 8088 ft. in elevation. Other owl species located, in order of abundance, were northern saw-whet (*Aegolius acadicus*), great horned (*Bubo virginianus*), barred (*Strix varia*), great gray (*Strix nebulosa*), and a western screech owl (*Otus kennicottii*). Surveys are recommended for at least 3 more years in the Little Belt Mountains to accurately determine the population characteristics and habitat used by boreal owls.

INTRODUCTION

The boreal owl (Aegolius funereus) is a highly nocturnal owl which inhabits northern hemisphere coniferous forests around the world. They are generally 21.5 to 30.5 cm long (Farrand 1983) and weigh 100-140 gm (Earhart and Johnson 1970). Boreal owls are small, brown owls with many white spots on their crown, nape, and back. Yellow eyes and a yellowish bill are framed by distinctive black facial frames which are spotted with many small white spots. Their white underparts are streaked with chocolate brown. Juveniles are dark chocolate brown with white spots across the back and white eyebrows and cheek spots.

Boreal owls are secondary cavity nesters, usually occupying cavities constructed by the northern flicker (Colaptes auratus) or pileated woodpecker (Dryocopus pileatus). Boreal owls will also use artificial nesting boxes (D. Genter per. comm.). Boreal owls are territorial and a nesting pair will actively defend the area around the nest site (D. Genter per. comm.). After the courtship in March and April, 4 to 6 pure white eggs are laid. The eggs are incubated for 27-28 days by the female and the young fledge 28-33 days after hatching (Terres 1980). Boreal owls prey mainly on small mammals, primarily redback voles (Clethrionomys gapperi) but also pocket gophers (Thomomys talpoides), shrews (Sorex spp.), and deer mice (Peromyscus maniculatus). Some insects and birds are also eaten (Hayward et al. 1987).

The owls are generally secretive throughout the year, residing

the call playback technique (Fuller and Mosher 1981) from vehicles, snowmobiles, and skis along selected survey routes between February 21 and March 27, 1991. Survey routes were primarily at elevations higher than 5000 ft. and in areas with large patches of old growth forests (Figure 3). Routes were selected and prioritized based upon conversations with Forest Service Biologist Don Sasse.

Surveys were started one half hour after sunset and lasted approximately 4 to 5 hrs, weather permitting. Playback stations were one half to 1 mile apart along the survey route. The spacing varied widely on some routes due to the topographic and/or habitat variation. Some survey routes were completed in their entirety on a single night, others were completed in segments surveyed on different nights. Therefore some segments of survey routes overlapped and were surveyed more than once, other portions only once. Time and estimated wind speed and direction were recorded at each calling station. Temperature was recorded at the first and last calling station each night. Elevation of each calling station was determined from topographic maps. At each station we listened for calling owls for 2 to 3 minutes, played 1 species call in all 4 directions for 2 to 3 minutes, listened for 2 to 3 minutes, and then repeated the procedure. Boreal owl calls were played most often, but occasionally great gray (Strix nebulosa) or northern saw-whet (Aegolius acadicus) calls were also used depending on habitat and calling responses. Survey report forms were completed for each survey conducted and owl observation forms were completed for each owl heard (Appendix 1). All calling points and owl

locations were recorded on 7.5 minute U.S.G.S. topographic maps along with the date and time for each calling point and observation (Appendix 2). Calling points were numbered with the route number followed by the calling point number. Owl locations were described according to the timber type of the stand the owl was located in. These types are named for the major volume species in the stand, regardless of tree size, and other species of trees may be present.

RESULTS

Surveys were conducted on 19 nights during the survey period. Weather, especially wind, caused some of the 19 surveys to be cut short and resulted in total survey cancellation on other nights. A total of 15 survey routes were established which totaled 70.2 miles and encompassed 87 calling points. The total number of miles surveyed was 82.6 miles (Table 1). The elevation of calling points ranged from 4720 ft. to 8088 ft. Temperatures during the surveys ranged from 14 to 36 degrees Fahrenheit.

Boreal owls were detected at 8 calling points with a minimum of 6 birds detected. Northern saw-whet owls were the most common owl detected, being heard at 12 stations with a minimum of 14 birds detected. Seven great horned owls (Bubo virginianus) were detected at 5 stations. Two barred owls (Strix varia) were repeatedly located in one area from 3 calling stations and a great gray owl and western screech owl (Otus kennicottii) were located at one calling point each. One unknown owl call was heard at one calling station (Table 2).

Boreal Owl Detections

Boreal owls were located at elevations from 6,400 ft. to 8,080 ft. Aspects of owl locations ranged were 3 on south facing slopes, 2 on west facing slopes, and one each facing northwest, north and northeast. All were located in response to song playback. All boreal owls located were in lodgepole pine stands except for one in a whitebark pine stand.

Calling point 7-009, 2/24/91, 8:45 pm, Moose Creek Route.

✓ This was the first owl we detected. The owl responded to song playback after the second calling sequence and continued to call until we left the area. It was located on Moose Creek near the confluence of Moose Creek and Rocking Chair Creek (T13N,R7E,sect.24,SW1/4,NE1/4) at 6700 feet. The owl's location was estimated to be in stand 711-06-85 which is classified as lodgepole, well stocked.

✓ Calling point 7-026, 2/26/91, 11:00 pm, Moose Mountain Ridge Route. This owl was heard while skiing to the next calling point after completing a calling sequence. The owl was located at approximately 7840 feet (T12N,R7E,sect.2,NE1/4,NE1/4), then moved up to the ridge (T13N,R7E,sect.36,SW1/4,SW1/4) at 8,080 feet and called again. It continued calling until we tried song playback again five minutes later. The owl was initially located

in stand 709-02-20 which is classified as mixed conifer, well stocked, and flew in response to song playback to stand 709-02-02, lodgepole, poorly stocked.

Yes - also SWO
702-02-42
06
Calling point 7-034, 3/8/91, 10:25 pm, Highway Route. This owl was heard after the second playback sequence. The owl responded only twice so the location is not precise. We estimated that the owl was located at the bottom of Deadman Creek (T12N, R8E, Sect. 23, NE1/4, SW1/4) at 6400 feet. The owl ceased calling when a northern saw-whet owl started calling near the calling point. The boreal owl was estimated to be in stand 702-02-42 which is lodgepole, medium stocked.

Yes -
702-04-29
Calling point 7-037, 3/11/91, 11:00 pm, Highway Route. We located this owl near the highway at the top of Kings Hill Pass near the Forest Service rental cabins (T13N, R8E, Sect. 34, E1/2, SW1/4). The owl responded to the initial song playback and was located immediately south of the calling point within 200 ft. The owl called a number of times and appeared to move around the edge of the hill while we were listening. This owl was located in stand 702-04-29 which is lodgepole, well stocked.

Yes -
Calling points 7-053 and 7-054, 3/13/91, 11:33 pm to 12:07 am,

Higgins Park Route. We heard this owl in response to initial playback at both calling stations. It remained in the same location (T12N,R8E,Sect.36,NW1/4,SE1/4), and called vigorously. This was the only boreal owl located in a whitebark pine stand, stand number 701-02-04, and was the only boreal owl that did not move in response to song playback. This was also the only location where we heard a boreal owl and great horned owls in close proximity.

✓ Calling points 7-065 and 7-066, 3/15/91, 10:04 pm to 10:37 pm, Williams Park Route. This location provided the only visual observation of a boreal owl during the survey. The owl was initially heard giving an OOO-WEE call at calling point 7-066 (T13N,R6E,Sect.20,NE1/4,NE1/4). The owl then followed the surveyors to the next calling point 7-065 (T13N,R6E,Sect.16,SW1/4,NW1/4), where it was observed calling in a tree adjacent to the road. There the owl was heard giving the typical winnowing call. The owl was initially located in stand 713-05-009, which is classified as lodgepole, well stocked and moved to stand 713-05-29, which is also classified as lodgepole, well stocked.

DISCUSSION

Intensive studies by Hayward et al. (1987) and Bondrup - Nielson (1984), show only potentially breeding males call, implying that the presence of calling owls indicates a breeding population. Therefore, the presence of calling boreal owls in the study area indicates that boreal owls nest in the Little Belt Mountains. The results of this survey should only be considered an indication of boreal owl activity and locations since the data gathered cannot be used to provide estimates of population levels or density within the study area.

Factors affecting the responses of boreal owls to call playback survey techniques are numerous. The single most important variable negatively affecting response is wind (Smith 1987 and Palmer 1987). We experienced numerous evenings that the wind canceled or shortened surveys and therefor we did not cover some areas that we feel have potential for boreal owl observations. The only previous surveys attempted on the district ended without any calling on three nights due to high winds and snow (Escano 1984).

All boreal owl locations in this survey except one were in timber stands classified as lodgepole. The other was in a whitebark pine stand. These findings are different than those found in the Bitterroot Divide (Holt and Hillis 1987), central Idaho (Hayward et. al. 1984), and southwest Montana (Mullen 1990) which all found boreal owls in spruce/fir forest types, although Escano (1984) reported that surveys on the Beaverhead National Forest located 4

boreal owls in lodgepole pine habitat types with scattered meadows or grass/sage openings. This discrepancy with the prevalent habitat type reported may be due to the limited amount of spruce/fir stands available at higher elevations in the Little Belt Mountains, or may be a factor of the habitat classification methods used in this survey.

Boreal owls in the Little Belts may have problems with warm summer temperatures since boreal owls are easily heat stressed (Hayward et al. 1987). Therefore, dense stands of timber which would provide cool moist sites for roosting may be important to boreal owls in the Little Belts. Also, the high level of wood cutting on the district (Sasse pers. comm.) may limit the availability of suitable nesting snags for boreal owls. Hayward (pers. comm. in Mullen 1990) suggested that clearcuts may provide edge habitat used by owls for hunting. However, Mullen (1990) warned that man-made openings also are often accompanied by the potential for increased human disturbance and the invasion of competing owl species, especially great horned owls.

Boreal owls have extremely variable calling activity (Hayward et al. 1986, Palmer 1987). Variations in prey populations directly influence calling activity by reducing breeding activity during periods of low prey populations (Hayward 1987). Bondrup and Nielsen (1978) found that pair formation will also cause the male to stop calling. Hayward (1983) noted that one male did not respond to surveys during the normal courtship period because he was already paired. Palmer (1987) found courtship periods ranging from 4 to 59

days with the longest courtship periods found for unpaired males. The variability in boreal owl calling activity shows that we can not effectively determine population dynamics of the boreal owl in the Little Belts from 1 survey season.

CONCLUSIONS AND RECOMMENDATIONS

This survey confirms that boreal owls are present in the Little Belt Mountains and expands the known range of the boreal owl into the isolated mountain ranges of central Montana. Hayward (1987) noted that the potential vulnerability of local populations to extinction depends upon the degree of interchange among demes. Determining and providing for the required degree of interchange may be especially important to populations in isolated mountain ranges such as the Little Belts. Boreal owls may also be present in the other isolated mountain ranges of central Montana such as the Crazy, Castle, Snowy and Judith Mountains. Surveys in the proper habitats in these mountain ranges would be beneficial to determine the eastern extent of boreal owls in Montana and the geographical relationship of boreal owl populations to one another.

Further investigations into the exact vegetative composition of the stands owls were located in would be beneficial. Since boreal owls generally use only conifer snags over 21" diameter at breast height in forested stands as nesting cavities (Hayward 1990), an upper size limit for conifers cut for firewood in high elevation areas may be considered. Small mammal surveys should also be conducted to determine the small mammal species occupying the

Little Belts that may be prey items for boreal owls.

As Mullen (1990) pointed out, short term surveys such as this do not take into account the yearly variation in boreal owl calling rates and any management directed solely by this one year of study may be harmful. Additional survey years may yield owl observations in areas that did not result in boreal observations this year. At least 4 years of surveys should be conducted to effectively ~~determine boreal owl distribution in the area~~ (Mullen 1989). Repeat surveys and additional surveys should be conducted, extending through April to better cover the study area. Emphasis should be placed on locating nest sites to gain a better idea of breeding habitat in the Little Belts.



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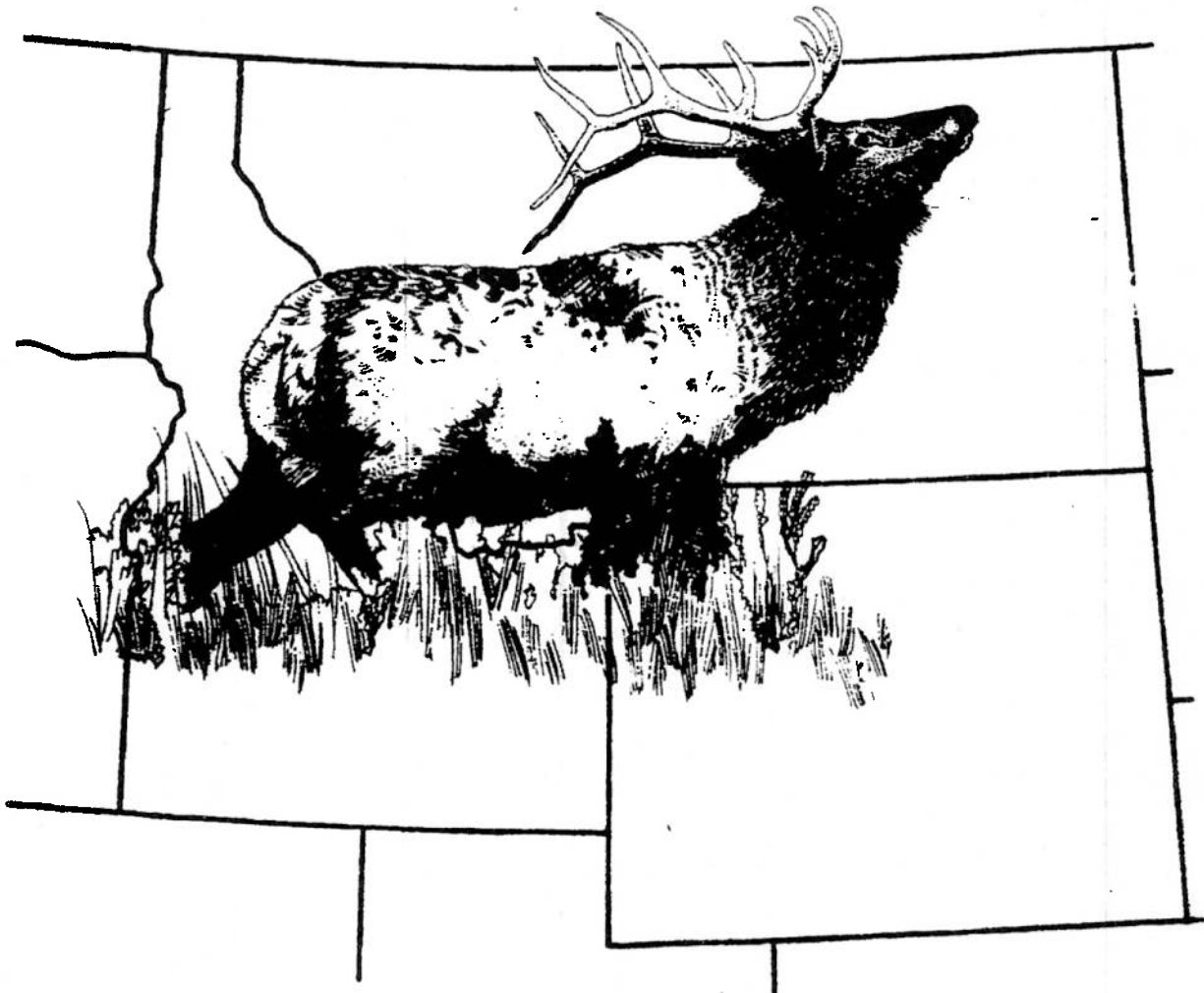
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Elk Manageme Northern Region: Considerations in Forest Plan Updates or Revisions

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Elk Management in the Northern Region: Considerations in Forest Plan Updates or Revisions

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INTRODUCTION

In the West, a large percentage of elk habitat is managed by the Forest Service, U.S. Department of Agriculture. Elk are a giant economic factor in Montana and Idaho, easily accounting for over \$100 million annually for hunting alone. This activity is especially important to many small, rural communities. At the same time, elk management can be controversial where it conflicts with other resource activities such as grazing, logging, and public access. As the habitat manager for this valuable resource, the Forest Service must develop management programs based on the best available information, work closely with State game managers, fully inform the public and disclose the effects of management actions, and embrace implementation of an ecological approach to elk management.

When the initial forest plans were developed in the early 1980's, there was no cohesive direction identifying a common set of elk management standards. As plans were written, generally recognized key pieces of elk management information were creatively modified by virtually every forest in an attempt to meet local needs. This often resulted in adjacent forests having startlingly different goals, objectives, standards, guidelines, and terminology.

In these forest plans, the approach to elk was usually narrow and focused. Because elk was a regional indicator species, managers established population targets, habitat standards, and monitoring goals. We recognize now that elk are part of a bigger picture and that elk habitat management must be placed within the context of ecosystem management, biodiversity, State management strategies and goals, and shifting public demand and interest that now embrace non-consumptive and consumptive interests.

This problem has been recognized and a solution proposed for the Northern Region of the Forest Service. Common terminology, a new perspective on elk vulnerability, and a better understanding of the application of habitat effectiveness have created the opportunity for forests to be more consistent and in tune with State management objectives. In the interest of better elk management, it is imperative State plans and forest

plans address the same issues. Elk vulnerability is the framework issue.

We present an initial overview under which individual forests can creatively address elk management and yet retain consistent and cohesive approaches within regional and State boundaries. Emphasis has been placed on process, content, and implementation of new information rather than on numerical standards, although these remain important for measuring success. Specific process guidance for biologists in the Northern Region of the Forest Service is provided in the appendix.

KEY COMPONENTS OF ELK MANAGEMENT

The relationship between National Forest lands and elk needs to be recognized for the following key components:

1. Habitat in which elk grow, reproduce, and exist as elements of biological diversity.
2. The basis upon which State management programs depend. While hunting mortality accounts for upward of 90 percent of elk mortality, the States depend on habitat availability and condition for their programs to exist.
3. Sites for the public to have the opportunity to hunt and view elk. Recreation is an important product of National Forest lands. In most areas, use of forests peaks during fall hunting seasons, but in other areas wildlife viewing is a year-around product. The setting needs to be considered along with other habitat issues.
4. Maintenance of elk as a part of the natural community and recognition of elk habitat in a landscape context and in response to natural processes.

These key components can be recognized and evaluated in the following three types of habitat considerations:

Habitat effectiveness: This is a measure to be applied to nonhunting, summer and fall habitat situations. It was developed from research related to the ability

of habitat to meet elk needs for growth and welfare requirements. It has been consistently misapplied as a measure of security during hunting season.

Elk vulnerability: This deals with security for elk during the hunting season. There is a rapidly expanding body of new information relating to this management concept that will be available for inclusion in forest plans as they are updated, revised, or amended.

Winter range: This has been a collective term referring to elk habitat during the nonsummer and fall, nonhunting season. However, during some years elk will move to winter habitat during the fall hunting season and, in most situations, become vulnerable. In updates, revisions, or amendments we must recognize and deal with this possibility as well as deal with traditional considerations.

HABITAT EFFECTIVENESS

Summer range includes the habitat used by elk from about late green-up (May) until they move to winter ranges, but prior to the hunting season. Summer range is the complete matrix upon which elk herds depend for growth, reproduction, and thrift. Management focus is on maintaining the ability of the habitat to meet elk needs for forage, water, seclusion, and special features (such as licks and moist areas). Forest Service lands that support summer range are the basis for State elk management; specifically, if habitat is degraded or poorly managed, the elk population will be degraded and, thus, directly influence State elk population management programs.

Habitat effectiveness is defined as the percentage of available habitat that is usable by elk outside the hunting season (Lyon and Christensen 1992). This is the measure of success in meeting elk needs on summer range. Based on years of research from various sites in Montana and Idaho, relatively sophisticated technologies exist for calculating habitat effectiveness. In forest plan revisions, updates, and amendments, this term should be used as a measure of summer range ability to support elk. Sources of information for habitat effectiveness and the major factors that influence it are included in Irwin and Peek (1979), Legee (1984), Lyon (1983, 1987), Lyon and others (1985), Thomas and others (1979), and Wisdom and others (1986). (See the References section at the end of this publication.)

Considerations for Forest Plans Related to Habitat Effectiveness

The following list is not inclusive but does cover the main issues managers need to consider.

1. **Roads**—density (miles per square mile), construction standards, seasons of use, method of closure.

2. **Special features**—wet sites, riparian habitat, licks, movement corridors.

3. **Cover**—extent, shape, size, connectiveness.

4. **Scale of analysis**—site specific, herd unit, habitat analysis unit.

5. **Spatial relationships**—intermingled ownerships, adjacent administrative units, district or forest "averaging."

6. **Domestic livestock**—forage and spatial competition.

Recommendations

Roads—Roads are undoubtedly the most significant consideration on elk summer range.

1. Use figure 1 (Lyon 1983) road model for determining habitat effectiveness related to roads. Avoid classifying roads as primitive and downgrading their effect unless they really are.

2. Discuss methods of closure. For elk, physical closure with "trashing" is desirable for year-long closure. Area closures are needed where terrain features and cover characteristics do not favor closure with gates or barriers. Honor systems of closure have been only moderately successful, at best.

3. Discuss construction standards. Where roads will be system roads, strive for construction and design features that lay lightly on the land. Identify temporary roads where they are an option. Avoid "tie through" systems where possible. Strive for minimum miles of new construction in summer range. Identify logging technology that reduces road construction. Avoid key habitat features when locating roads.

4. Any motorized vehicle use on roads will reduce habitat effectiveness. Recognize and deal with all forms of motorized vehicles and all uses, including administrative use.

5. Levels of habitat effectiveness:

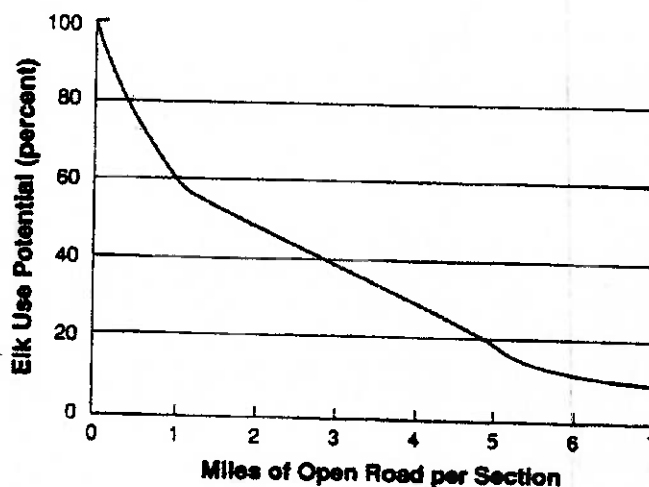


Figure 1—Habitat effectiveness for elk determined by road density (Lyon 1983).

0.757 2 2 m
500

a. For areas intended to benefit elk summer range and retain high use, habitat effectiveness should be 70 percent or greater.

b. For areas where elk are one of the primary resource considerations habitat effectiveness should be 50 percent or greater.

c. Areas where habitat effectiveness is retained at lower than 50 percent must be recognized as making only minor contributions to elk management goals. If habitat effectiveness is not important, don't fake it. Just admit up front that elk are not a consideration.

d. Reducing habitat effectiveness should never be considered as a means of controlling elk populations. A population over target is not a Forest Service habitat problem. Remember that in most situations, populations can be reduced through hunting.

Special Features—Wet drainage heads, saddles, riparian habitats, shadowed draws with cool air movement, and wet meadows are some examples of special features. In many areas these features support a disproportionate level of elk use and contribute significantly to overall elk use of a larger area. Generally, these sites are highly desirable for forage, water, temperature regulation, movement, or a combination. Such sites should be recognized and protected in prescriptions that deal with elk summer range. Logging activities, road locations, and siting of structures or activities should all be evaluated. Avoid damaging these features where elk are a benefiting resource (Lyon and others 1985).

Cover—Early guidelines greatly emphasized analysis of cover, specifically thermal and hiding cover (Thomas and others 1979). Today, detailed analyses of hiding and thermal habitat components are not considered as essential except in habitats with high natural levels of openings or where conifer cover is at a premium. Some approaches have created the classification "optimal cover" (Wisdom and others 1986) as an aid in analyzing cover from aerial photographs. Another approach, where stand analysis data are available, is provided by the HIDE2 hiding cover computer model (Lyon 1987).

While we still need to recognize the importance of maintaining cover blocks and movement corridors, a more meaningful approach to cover analysis includes maintenance of security, landscape management of coniferous cover, and monitoring elk use with radio telemetry or other means. Recognition that summer cover blocks are also fall hunting season security areas is an important coordinating consideration.

Cover unit size, patterns on a landscape basis, connectivity with other cover, the amount of cover available to elk, and known use patterns by elk should be considered in prescriptions.

Scale of Analysis—Early guidelines tended to be project specific in scale; often 3,000 to 10,000 acres

was recommended. However, while road locations, special features, and the location of cover or cutting units still need project-level analysis, such analysis also needs to recognize the project in a broader context of herd units (where known), habitat analysis units, or other meaningful, larger scale perspectives. Herd units need to be identified in cooperation with State biologists. Consideration of project-level effects may necessitate analysis in light of influences on adjacent herd units, adjacent forests, or even adjacent States over landscape units from 30,000 to 150,000 acres.

Another consideration in establishing factors for scales of analysis are known movement patterns. If your management of summer range may influence elk in terms of their movement to adjacent fall or winter ranges, the scale of analysis should be appropriate.

Spatial Relationships—This criterion has to do with habitat features, values, or project analyses that have a relationship to intermingled ownerships, concurrent and adjacent activities, or adjacent features that are significant to your concerns for elk habitat.

When elk habitat crosses intermingled ownerships, activities that reduce habitat effectiveness on intermingled lands require the Forest Service to decide how they will be dealt with in prescriptions. Adjacent and concurrent activities beyond Forest Service control, such as logging and grazing on private land, should be recognized in prescriptions, and courses of action for the Forest Service should be identified. Federal managers need to coordinate with State biologists on these activities.

Internally controlled activities that affect elk summer range should also be recognized. An example is the relationship of herd units or analysis areas to each other and, collectively, to forest elk habitat. Each individual unit should have an identified role for elk and a level of habitat effectiveness. In this way, the whole area or forest can achieve an expected level. It is undesirable to play off one unit against another. For example, recognizing high habitat effectiveness values in adjacent wilderness areas should not be a justification for excessive reductions in habitat effectiveness in managed areas, even if some average level for the forest is met.

Significant reductions in habitat effectiveness in areas identified as benefiting elk cannot be recovered at a pace equal to our ability to move activities around a forest. In addition, patterns of recreational activity related to elk can be significantly affected by this type of management.

Domestic Livestock—Current perspective is that cattle on elk summer range are not as significant a conflict as formerly thought and probably only warrant analysis where local understanding indicates a problem may exist. Elk appear to avoid areas where cattle

are present if other options exist. Where no other options exist, elk will tolerate some cattle use.

Major points of conflict are wet sites and gentle terrain with succulent vegetation. Season-long cattle occupation of these types of sites undoubtedly reduces their value to elk.

Forests where cattle are a concern need to work with State biologists on standards and guidelines for cattle and elk relationships.

Of equal concern is the perception that elk herd expansion is causing cattle use reductions on National Forests. In developing management guidance, forests should address this issue and strive to gather habitat use data that will help clarify this situation.

Summary for Summer Range

1. Habitat effectiveness is the method of measurement.
2. The presence and motorized use of roads is the major impact on elk habitat effectiveness.
3. Detailed cover: forage analysis is important only when cover is at a premium.
4. Landscape levels of analysis are necessary.
5. Recognition of adjacent activities, intermingled ownerships, and cumulative effects is needed in plan revisions and updates.
6. Analysis of elk and domestic livestock conflicts is probably warranted where it is considered a problem locally.
7. Forests should set standards for habitat effectiveness that are congruous with goals for a prescriptive unit. Specific prescriptive guidelines should reflect the level of habitat effectiveness desired.
8. Close coordination with State biologists and recognition of identified State management goals for elk are necessary in all aspects of summer range management.
9. Forests should recognize traditional uses of elk as well as burgeoning nonconsumptive interest in elk.

ELK VULNERABILITY ANALYSIS

The primary source of elk mortality is hunting. While the State manages hunters, the Forest Service management of access and cover are extremely influential in affecting the ability of hunters to kill elk. Therefore, it is important that in forest plan revisions or updates, prescriptive guidance is identified for elk vulnerability analysis. This procedure applies during the hunting season and is not to be confused with habitat effectiveness. Vulnerability is a separate issue that forests need to recognize in elk management and write into prescriptions. Vulnerability results from an extremely complex relationship involving access, cover, topography, hunter density, and weather. A great deal of intercorrelation among these factors

exists, and a great deal of cooperation between agencies will be necessary to achieve the goals of elk vulnerability management.

The measure of success for elk vulnerability is the level of compatibility between Forest Service and State management plans. Often, this will be the number of bulls per hundred cows surviving the hunting season or some expression of the quality of the recreation experience provided.

Considerations for Forest Plans Related to Elk Vulnerability

The following list is not inclusive but does include the main issues managers need to consider:

1. *Roads*—season of use, density.
2. *Security areas*—distance from roads, size, cover characteristics, closures (area), topographic characteristics.
3. *Cover management*—description, connectiveness, scale, terrain relationships.
4. *Mortality models*—demonstrated predictors of elk mortality based on habitat quality, hunter density, or other factors.

Recommendations

Roads—As with habitat effectiveness, access to and use of roads appear to be the most significant factors in vulnerability analysis.

Two studies in Idaho have demonstrated direct relationships between levels of road access and bull mortality (Leptich and Zager 1991; Unsworth and Kuck 1991). In Montana, Youmans (1991) implicated "road densities as the key factor in increased elk vulnerability."

Concerning open roads during hunting season, forests should develop criteria that meet State management goals for elk. Information on the relationship between roads and elk vulnerability is so new that specific criteria are scarce. However, the studies in northern Idaho provide initial guidance. Unsworth and Kuck (1991) found bull survival more than doubled in situations comparing road densities in excess of 4 miles per section with densities under 0.5 mile per section. In a different study area, Leptich and Zager (1991) reported bull mortalities of 62, 45, and 31 percent in study areas with 4.5, 2.6, and 1.0 miles of open road per section. In both these studies, cover during the hunting season was not considered limiting.

1. In areas with heavy cover, road management can be extremely influential in meeting desirable post-season bull:cow ratios.
2. Where heavy cover is not available, reduced open road densities contribute to maintaining some level of quality hunting opportunity through the season and to meeting postseason bull:cow ratios. In areas of

more open cover and, perhaps, gentler terrain, roads speed up the harvest of available bulls and make bulls more vulnerable throughout the season. Increased emphasis should be placed on security where poor cover conditions exist.

3. Even primitive roads that see little summer use are often used extensively during the hunting season. Area closures with open routes designated will most likely provide better security than individual closures. Area closures should address all motorized vehicles including all-terrain vehicles.

Security Areas—Security is the result of a combination of factors that allow elk to remain in a specific area while under stress from hunting. In Forest Service management, such areas are defined by cover blocks and road management. Specifically, these are areas of coniferous cover large enough and far enough away from open roads to provide security. There have been efforts on the Lolo and Deerlodge National Forests to develop criteria for managing security. The "Hillis paradigm" (Hillis and others 1991) provides these criteria and, with careful consideration, may be appropriate for other forests to use as a general guide. Briefly, this model identifies the size (250 or more acres), shape (nonlinear), and distance from open roads (over 0.5 mile) for security areas as well as how much of the area (over 30 percent) should be dedicated to security.

In discussions with biologists in Idaho and Montana, there appears to be a gradient from west to east regarding the significance of cover in this equation. In northern Idaho, it appears that open road density, hunter numbers, and topographic roughness are the major considerations (Unsworth and others 1993). Cover is so ubiquitous that security can be controlled with road management alone. As you move east into Montana and over the Continental Divide, cover considerations become more important because cover is less abundant and less contiguous. It is extremely important for forest biologists to work with their State counterparts in developing criteria for security areas, including their size, extent, distance from roads, and vegetative characteristics. Data from radio telemetry studies are the best source for developing such criteria.

Cover Management—This criterion is directed mostly at the more naturally open elk habitat in central and southwestern Montana and southern Idaho where care must be taken to recognize and retain adequate coniferous cover. In developing this criterion, a landscape-level perspective is absolutely necessary. Size, location on the landscape, connectiveness with other cover, and vegetative composition are important considerations (Hillis and others 1991). Data from Montana hunting seasons suggest that elk are less selective about the specific vegetative characteristics of coniferous cover and more responsive to size of units, connectiveness with adjacent units, and the scale of

cover on the landscape (Lyon and Canfield 1991). A strong relationship exists between maintaining cover for summer range habitat effectiveness and maintaining the same cover for security during fall hunting. Where coniferous cover may be a limiting factor, it will be important to develop long-term perspectives (rotation length) on cover management that address condition, quantity, location, and configuration.

Mortality Models—Models that link habitat, hunter density, and elk mortality can provide guidelines to coordinating habitat condition and State management objectives. Unsworth and others (1993) have developed a model for northern Idaho that predicts bull elk hunting season mortality using open road density, circular standard deviation of aspect, and hunter intensity (density for the length of the season). This model virtually requires a computerized Geographic Information System for calculating the aspect variable. But the effect can be estimated based on the fact that greater topographic relief reduces elk vulnerability. The more moderate the topography (fig. 2), the more impact road density and hunter density have. If we assume average topography and around 10 hunter days per section spread over a 26-day season, the probability of mortality for a bull elk is 60 percent greater in an area with 1 mile of road per section than in an unroaded area. Likewise, 2 miles of road per section will more than double the mortality probability, and at higher road densities bulls usually do not survive the hunting season.

Using a different measure of hunting intensity, Vales and others (1991) and Vales (1993) presented data from northeastern Oregon indicating that the ratio of hunters to available elk can also provide an estimate of probable mortality; basically, there is a consistent increase in harvest rate as the number of hunters per elk increases (fig. 3). These data are important because they indicate that excessive hunting pressure can, in the end, overwhelm all other provisions of elk vulnerability management.

Summary for Elk Vulnerability

1. Roads appear to be the single most important variable that the Forest Service manages. Roads not only directly affect elk mortality but also affect hunter opportunity by accelerating bull mortality. Forests must work closely with State biologists to identify acceptable levels and locations of motorized access to meet postseason bull:cow ratios and maintain optimum hunter opportunity.

2. Security area definition is variable across the region. Some forests have developed criteria. It is essential that cooperation and coordination with State biologists be used to formulate criteria.

3. Elk vulnerability analysis, a new concept, will be further defined. Hunter density and opportunity

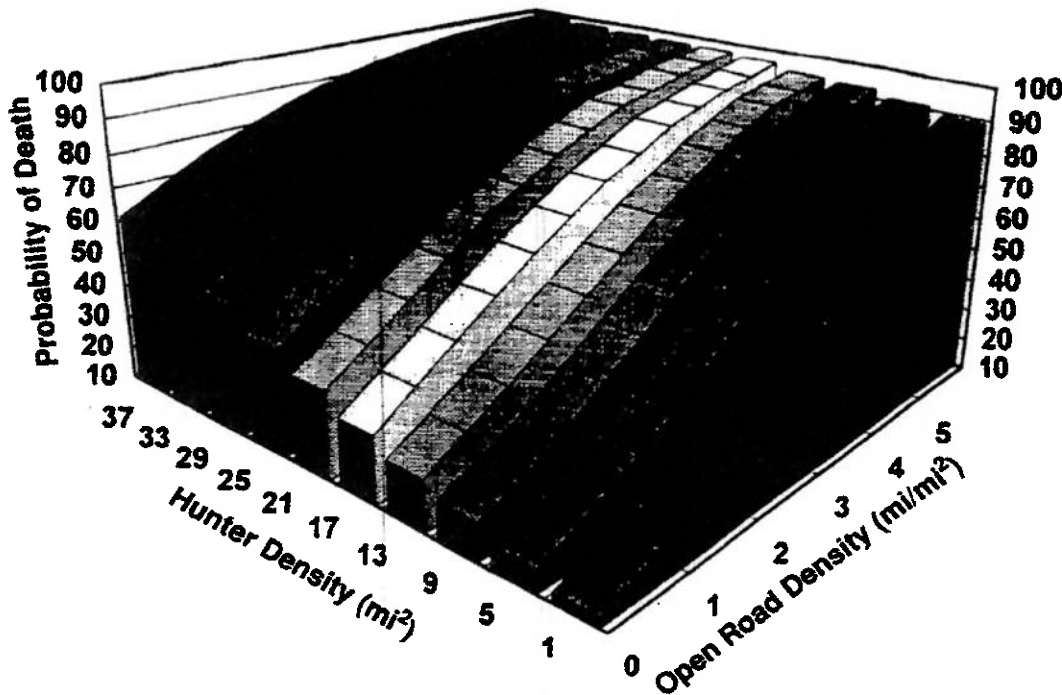


Figure 2—Elk vulnerability influenced by hunter density and road density (Unsworth and others 1993).

afforded by State regulations are also major components. It is essential that forest biologists and planners and their State counterparts communicate and coordinate extensively on this topic as forest standards and guidelines are developed.

4. Recently available mortality models can establish numerical standards for elk mortality. Local data bases may exist to help tailor mortality models to specific geographic areas. Numerical standards for elk mortality can be established through coordination with State biologists.

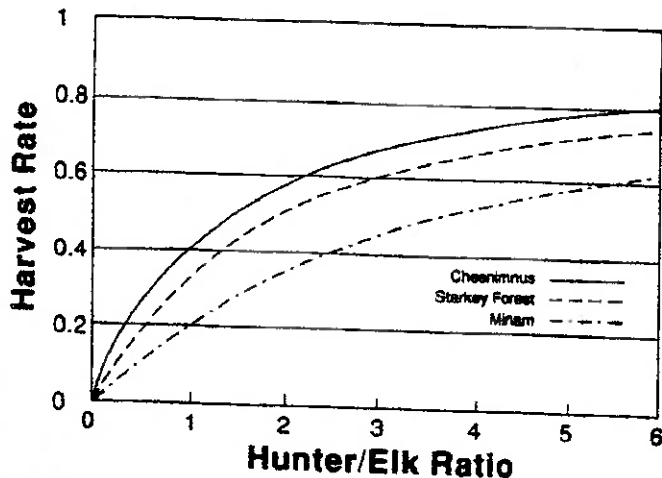


Figure 3—Elk vulnerability influenced by hunter to elk ratio (Vales 1993).

WINTER RANGE

Management of winter range remains the single most site-specific consideration for elk habitat. Each winter range is unique in some way. In this section, we briefly address the traditional considerations that already appear in the majority of forest plans. We again mention, however, that winter range should be evaluated as a part of the vulnerability assessment where appropriate to do so.

Traditionally, winter ranges for elk have been viewed as geographic sites on which animals concentrate seasonally because of snow depths. Heavy utilization of available plants, and animal die-off in severe winters, have been commonly recorded. For many years, the primary objective of management was to improve, or at least prevent deterioration of, existing vegetation.

In recent years, our understanding of animal physiology on winter ranges has modified this view. Forage is important, but in severe weather many animals substitute an energy-conservation strategy for forage intake. Thus, management of winter range to improve thermal cover and prevent harassment may be as important as anything done to change forage quantity or quality.

Considerations for Forest Plans Related to Winter Range

The following list is not inclusive but does include the main issues managers need to consider:

1. *Forage quantity and quality*—methods for improvement.
2. *Thermal cover*—energy conservation considerations.
3. *Roads and other disturbances*—energy conservation considerations.
4. *Livestock management*—forage allocation management.

Recommendations

Forage Quantity and Quality—In the majority of situations, actually modifying forage quantity or quality on the winter range is a difficult management challenge. Encroaching vegetation can sometimes be removed mechanically or with fire, and large or decadent shrubs can be burned to produce resprouting.

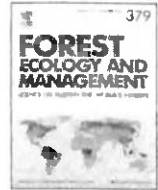
Thermal Cover—Some winter ranges lack thermal cover, which does not mean thermal cover serves no purpose where it is available. Where behavior patterns have been recorded, elk select resting and feeding sites based on control of energy transfer rather than forage availability. We recommend selective retention of larger trees where possible.

Roads and Other Disturbances—Disturbance and harassment result in tremendous energy costs to wintering animals. Selective road closures and restrictions on recreational use have proved effective in reducing these costs.

Livestock Management—Appropriate management of domestic livestock can, in some cases, be an important consideration in management of elk winter ranges. Local range specialists should be consulted about grazing techniques designed to leave adequate winter forage for elk.

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Mountain pine beetle attack faster growing lodgepole pine at low elevations in western Montana, USA

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ABSTRACT

Global change has impacted forests through altered disturbance regimes. In the western US, climate change has resulted in extensive and severe mountain pine beetle outbreaks. These outbreaks have the potential to impact forest function through the selection of certain phenotypes. We investigated the potential for bark beetle-induced selection by way of measuring growth and climate response in mountain pine beetle-killed and surviving lodgepole pine in the Northern Rockies. We had three objectives: (1) investigate differences in growth between beetle-killed and surviving lodgepole pine prior to a recent outbreak, (2) compare the climate-growth relationships for beetle-killed and surviving lodgepole pine and how those relationships explain observed growth differences and predict mortality risk, and (3) investigate growth differences and growth-climate relationships across north- and south-facing aspects and over an elevation range representing local climate gradients. Significantly higher growth rates were observed in beetle-killed trees at low-elevation sites, but not at mid or high elevations. While aspect influenced overall growth, it did not have a significant influence on the difference in growth between beetle-killed and surviving trees. Growth showed significant relationships with several climate variables (i.e., previous-year August temperatures, October temperatures, annual precipitation, and summertime climatic water deficit), with slight differences in those relationships between beetle-killed and surviving trees. Mixed effects models demonstrated that higher growth rates and age increased the probability of mortality during the outbreak at all elevations, and also that climatic water deficit and previous-year August maximum temperatures were related to the magnitude of growth differences between beetle-killed and surviving trees. Overall, mountain pine beetles tended to attack large, fast-growing, lodgepole trees, especially at lower elevations where trees may be more susceptible to seasonal water stress.

1. Introduction

Forests are globally important due to the ecosystem services they provide (Trumbore et al., 2015). Recently, widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have occurred in the western United States and Canada, resulting in mass mortality across large areas of forest (Meddens et al., 2012). These outbreaks are driven in part by changes in regional climate, where temperatures have increased and precipitation patterns have shifted (IPCC, 2014). Warmer and drier conditions stress host trees and provide a longer period of temperatures suitable to beetles (Dale et al., 2001; Raffa et al., 2008; Bentz et al., 2010). Thus, beetles are both more capable of reproducing rapidly and can more easily overwhelm tree defenses (Mitton and Ferrenberg, 2012). As water stress is predicted to increase in many ecosystems in the western US (Seager et al., 2007; IPCC, 2014), the need to more fully understand the relationship between host trees, bark beetles, and climate is significant. Specifically, it is important to

understand how host trees interact with climate and to determine the impact of those interactions on host tree susceptibility to beetle attack.

Mountain pine beetles are a native, 'irruptive,' insect in western North America. Beetles attack trees by burrowing through the tree's bark and into the phloem. Successful attacks occur when sufficient numbers of beetles are recruited to attack the tree via the release of pheromones by the initial attackers (Raffa, 1988). These mass attacks succeed by overwhelming tree defenses, and result in mortality of the host tree. Beetles also introduce blue-stain fungus to trees during attacks, which helps to kill trees by blocking the xylem with fungal spores. Tree defenses include producing resins to physically expel beetles and producing defensive compounds, processes that require a substantial investment of resources (Raffa and Berryman, 1983). Trees become more susceptible to successful attack when climate conditions are stressful because their resources are already limited (Waring and Pitman, 1983). Additionally, climate conditions that are stressful to host trees are typically beneficial to the beetles, with warmer

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The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution?

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Abstract: We propose a fundamental geographic distribution for the wolverine (*Gulo gulo* (L., 1758)) based on the hypothesis that the occurrence of wolverines is constrained by their obligate association with persistent spring snow cover for successful reproductive denning and by an upper limit of thermoneutrality. To investigate this hypothesis, we developed a composite of MODIS classified satellite images representing persistent snow cover from 24 April to 15 May, which encompasses the end of the wolverine's reproductive denning period. To investigate the wolverine's spatial relationship with average maximum August temperatures, we used interpolated temperature maps. We then compared and correlated these climatic factors with spatially referenced data on wolverine den sites and telemetry locations from North America and Fennoscandia, and our contemporary understanding of the wolverine's circumboreal range. All 562 reproductive dens from Fennoscandia and North America occurred at sites with persistent spring snow cover. Ninety-five percent of summer and 86% of winter telemetry locations were concordant with spring snow coverage. Average maximum August temperature was a less effective predictor of wolverine presence, although wolverines preferred summer temperatures lower than those available. Reductions in spring snow cover associated with climatic warming will likely reduce the extent of wolverine habitat, with an associated loss of connectivity.

Résumé : Nous présentons une répartition géographique fondamentale du glouton (*Gulo gulo* (L., 1758)) basée sur l'hypothèse selon laquelle la présence des gloutons est restreinte par leur association obligatoire à une couverture persistante de neige au printemps nécessaire pour le succès des terriers de reproduction, ainsi que par la limite supérieure de la thermoneutralité. Afin d'examiner cette hypothèse, nous mettons au point un assemblage d'images satellites classifiées MODIS représentant la couverture persistante de neige du 24 avril au 15 mai, ce qui englobe la fin de la période d'utilisation des terriers de reproduction chez les gloutons. Afin d'examiner la relation spatiale du glouton avec les températures maximales moyennes d'août, nous utilisons des cartes de températures interpolées. Ensuite, nous comparons et corrélons ces facteurs climatiques avec des données géographiques spatiales sur les emplacements des terriers de gloutons et les sites de télémétrie en Amérique du Nord et en Fennoscandie, ainsi qu'avec notre compréhension actuelle de l'aire de répartition circumboréale du glouton. Tous les 562 terriers de reproduction de Fennoscandie et d'Amérique du Nord se retrouvent dans des sites à couverture de neige persistante au printemps. Quatre-vingt-quinze pourcent des sites de télémétrie en été et 86 % des sites en hiver concordent avec la couverture de neige du printemps. La température maximale moyenne en août est une variable prédictive moins efficace de la présence des gloutons, bien que les gloutons préfèrent des températures d'été plus fraîches que celles qui sont disponibles. La réduction de la couverture de neige au printemps associée au réchauffement climatique va vraisemblablement réduire l'étendue de l'habitat du glouton, ce qui entraînera une perte de connectivité.

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species such as the wolverine, in which dispersing individuals are capable of moving long distances, spatial boundaries between metapopulations and extralimital movements can become difficult to distinguish (McKelvey et al. 2000). Wolverines were once considered to be continuously distributed throughout montane regions in the western US, but Aubry et al. (2007) found substantial gaps in the distribution of verifiable records of wolverine occurrence historically that corresponded to gaps in the distribution of alpine habitats and areas with persistent spring snow cover. Available evidence also indicates that connectivity among wolverine populations is essential for maintaining viability in fragmented portions of their range (Flagstad et al. 2004; Cegelski et al. 2003, 2006; Schwartz et al. 2007). Schwartz et al. (2009) found that restricting wolverine dispersal paths to areas defined by the presence of persistent spring snow cover improved correlations to patterns of genetic structure, indicating that successful dispersal was largely limited to paths within these areas. Therefore, at least in the western US, historical and current distribution; den sites; habitat use across sexes, ages, and seasons; and dispersals that lead to gene flow all occur within this bioclimatic envelope.

At the circumboreal scale, the spring snow coverage accords fairly well with the expert-derived range map (Fig. 1). Current wolverine range in North America differs from the area delineated by the spring snow coverage, primarily in regions where wolverines occurred historically but were extirpated during the 20th century, such as California, Colorado (Aubry et al. 2007), and Quebec (Slough 2007). In Eurasia, the species' current and historical ranges are less clearly understood. In some portions of the wolverine's putative historical range in Eurasia, habitat loss resulting from climatic changes in the past may have contributed to extirpations. This is particularly true before the mid-1800s, when average temperatures in the northern hemisphere were much lower (Salinger 2005). Both the Alps and the Carpathian Mountains contain areas with persistent spring snow cover and maximum summer temperatures consistent with wolverine climatic requirements (Fig. S2), suggesting that these montane systems may have supported wolverine populations historically. However, we lack reliable information on the wolverine's historical range in Europe or Asia. Consequently, montane areas at the southern extent of the spring snow coverage in Russia, Mongolia, and China represent high-priority areas for investigating both current and historical wolverine distributions, verifying wolverine use of snow for reproductive dens, and documenting seasonal shifts in elevation.

It is also important to recognize that the spring snow and summer temperature coverages are spatial models that incorporate interpolated and averaged data. In addition, the time period we used for the spring snow coverage (24 April – 15 May) was based on that used by Aubry et al. (2007). Although 15 May represents the approximate end of denning, the actual date likely varies geographically. We made no attempt to fit the snow coverage to either the collected data or the heuristically derived range map, but recognize that slight shifts in the analysis period result in significant changes in areal snow cover. For example, when we lengthened the time period by 1 week on either end (15 April – 28 May), the extent of the coverage declined by 3% in portions

of the western US. Thus, the spring snow coverage should be viewed as an approximation of underlying bioclimatic requirements.

Creating range boundaries heuristically incorporates errors of precision, accuracy, and interpretation (Brown et al. 1996; McKelvey et al. 2000; Hurlbert and White 2005). As an alternative, we refined the wolverine's circumboreal range using climatic conditions as explanatory variables for reproductive den site selection and year-round habitat use. The strong concordance of wolverine den sites with the spring snow coverage clearly reflects an obligatory relationship with snow cover for reproductive dens. The spatial concordance of wolverine telemetry locations with the summer temperature coverage supports the hypothesis that wolverines redistribute to cooler environments during hot summer months in southern portions of their range. The ubiquitous distribution of wolverines at northern latitudes, where temperatures remain low in the summer, provides additional support for this hypothesis. Consequently, we believe that the denning requirements of the wolverine primarily determine the limits of its circumboreal range, whereas temperature likely plays an important role in habitat selection occurring at finer spatial scales. In northern areas where these climatic factors represent less important limits, other more proximal factors such as prey or carrion availability and human persecution likely determine wolverine presence and habitat use.

If wolverine distribution in southern regions can be delineated reliably by persistent spring snow cover, climate-driven reductions in the size and connectivity of these areas may signal associated range losses for the wolverine. Significant reductions in spring snow cover associated with climatic warming have already occurred in some portions of the wolverine's range in the contiguous US (Mote et al. 2005). If these trends continue, habitat conditions for the wolverine along the southern extent of its circumboreal range will likely be diminished through reductions in the size of habitat patches and an associated loss of connectivity, leading to a reduction of occupied habitat in a significant portion of the species range.

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Introduction

The extent to which a species' geographic distribution correlates with climatic variables depends on the importance of those variables to the species' fundamental niche (Pearson and Dawson 2003). The influence of climate on the natural distribution of many species (Pearson and Dawson 2003) has led to the development of "bioclimatic envelope" models that relate range limits to sets of climatic conditions within which a species can survive and reproduce (Box 1981; Pearson and Dawson 2003; Thuiller et al. 2005; Lawler et al. 2006). Bioclimatic models consider climatic variables as correlates of a species' current distribution and are often used to predict range shifts that may result from different climate change scenarios (Hijmans and Graham 2006). These correlative approaches are sometimes criticized because they fail to account for interactions with biotic factors (Davis et al. 1998; Pearson and Dawson 2003; Heikkinen et al. 2006; Post et al. 2009) and may not accurately reflect the ecology, behavior, or physiology of the target species (Soberón 2007; Pöyry et al. 2008). Consequently, evaluating an organism's climatic requirements by correlating current range with climatic factors is problematic. However, if researchers possess reliable understandings of both an organism's geographic range and its climatically linked biological requirements, they can evaluate whether current range is consistent with the climatic conditions needed to fulfil those requirements. This is the approach taken here.

The wolverine, *Gulo gulo* (L., 1758), occurs throughout arctic regions and also in subarctic areas and boreal forests of Eurasia and North America. In southern portions of the wolverine's range in western North America, wolverine populations occupy peninsular extensions of boreal forests in montane regions. Our understanding of the wolverine's geographic distribution is informed by a relatively small number of radiotelemetry studies and monitoring programs in North America and Fennoscandia (Landa et al. 1998a; Flagstad et al. 2004; Lofroth and Krebs 2007), but these efforts are often limited in both spatial and temporal extent. Derived understandings of wolverine behavior and habitat use are influenced by the scale at which they are developed; understandings developed from within an individual home range (e.g., second- or third-order selection sensu Johnson 1980) may not be informative concerning factors that limit range at broader spatial scales (e.g., first-order selection sensu Johnson 1980). Only one study has attempted to define the wolverine's niche on a continental scale (Aubry et al. 2007).

Wolverine occurrence has been correlated with remoteness from human development (Banci 1994; Carroll et al. 2001; Rowland et al. 2003; May et al. 2006, 2008). However, historical records for western North America (the only portion of the wolverine's circumboreal range wherein the species' historical distribution has been thoroughly investigated; Aubry et al. 2007) reveal little evidence of wolverine presence outside subalpine habitats (Aubry et al. 2007) and support genetic evidence of long-term isolation in the Sierra Nevada (Schwartz et al. 2007). The only study to look at the wolverine's spatial relationship with human infrastructure (May et al. 2006) found spatial separation occurring at broad spatial scales but little evidence of avoidance at finer scales.

In montane regions, wolverines reportedly shift habitat

use to higher elevations during summer and lower elevations during winter. Moving up in elevation during the summer may provide a thermal advantage to wolverines (Hornocker and Hash 1981) when ambient temperatures are high, or may reflect seasonal variation in prey availability (Gardner 1985; Whitman et al. 1986; Landa et al. 1998b; Copeland et al. 2007; Krebs et al. 2007). However, Banci and Harestad (1990) reported no elevational shift in habitat use by wolverines in Yukon, Canada, hypothesizing that seasonal movements were unnecessary owing to low summer temperatures at low elevations and a scarcity of prey at high elevations. Although it is generally accepted that temperature influences the geographic distribution of animals, there have been few studies of the relationship between range limits and thermal tolerances (Clark 1996).

Snow is regarded as an important component of the wolverine's seasonal habitat requirements (Banci 1987; Magoun and Copeland 1998; Aubry et al. 2007). Well adapted to snow, the wolverine's compact body and large plantigrade feet aid in travel through soft snow, and its dense pelage provides insulation from extreme cold. It has been hypothesized that deep, persistent spring snow cover is an obligate component of wolverine reproductive denning habitat (Magoun and Copeland 1998) because it aids the survival of young by providing a thermal advantage (Pulliainen 1968; Bjärvall et al. 1978) and provides a refuge from predators (Pulliainen 1968; Persson et al. 2003). Reproductive denning begins in early February to mid-March, and post-weaning den abandonment occurs in late April and May (Landa et al. 1998a; Magoun and Copeland 1998; Persson et al. 2003). Reproductive dens may be located under boulders or downed trees buried beneath the snow (Magoun and Copeland 1998) or may be temporary structures within the snow layer itself (Lee and Niptanatiak 1996; Landa et al. 1998a, 1998b; Magoun and Copeland 1998). If persistence of wolverine populations is linked to the availability of suitable reproductive den sites (Banci 1994), snow cover that persists throughout the denning period may be a critical habitat component that limits the wolverine's geographic distribution.

Here, we investigate the hypothesis that wolverine distribution at the broadest spatial scale is constrained within a climatic envelope defined by an obligate association with persistent spring snow cover and by an upper limit of thermoneutrality. We test this hypothesis by comparing and correlating the locations of wolverine reproductive dens from throughout their circumboreal range, and telemetry locations from 10 recent wolverine studies in western North America and Scandinavia, with spatial models representing the distribution of spring snow cover and average maximum August temperatures. We contrast these findings with a heuristically derived map of the wolverine's current circumboreal range.

Materials and methods

Spring snow cover data

We developed a spatial data layer of spring snow cover in the Northern Hemisphere for a 7-year period from 2000 to 2006 using moderate-resolution imaging spectroradiometer (MODIS) classified daily snow data (500 m spatial resolution) from the Terra satellite (Hall et al. 2006). Terrestrial pixels were classified into four cover classes (snow, bare

Fig. 3. Distribution of wolverine dens in Sweden, Norway, and Finland overlaid on the spring snow coverage. The gradient in the spring snow coverage represents the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May.

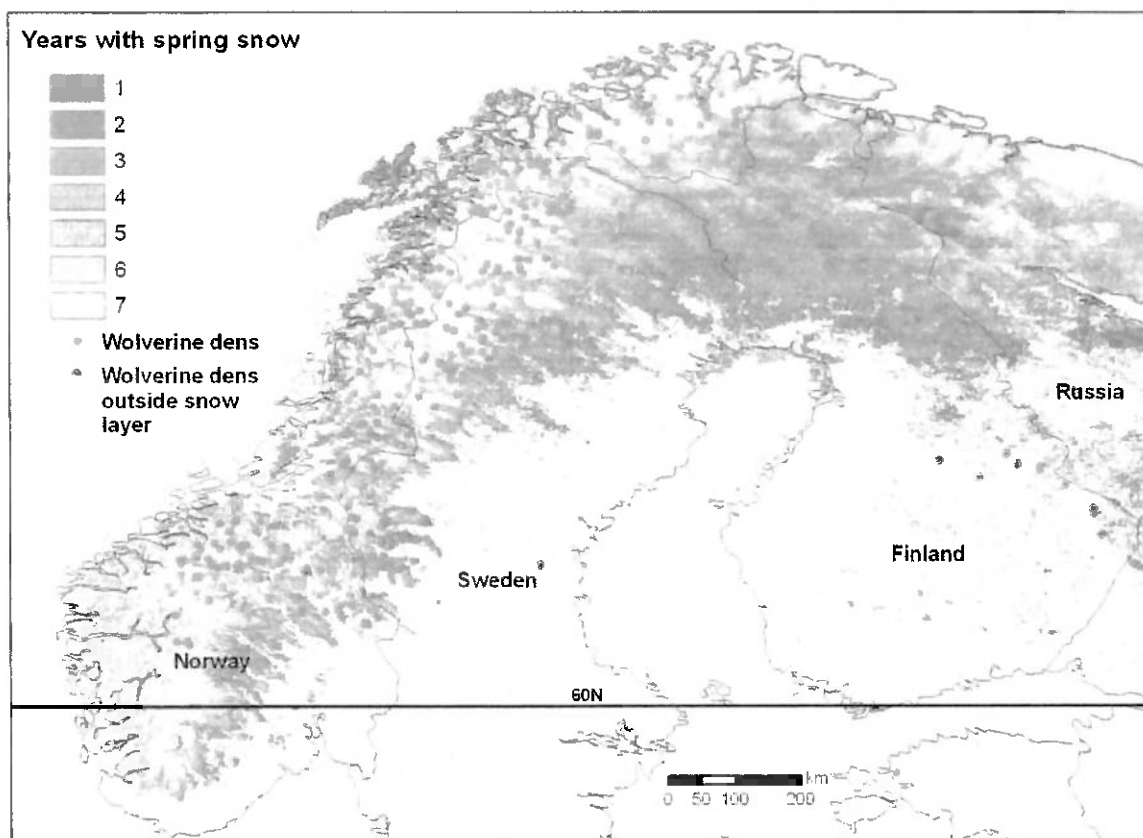
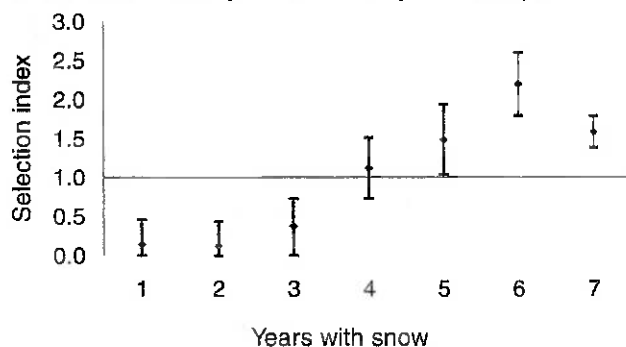


Fig. 4. Selection indices depicting the relation between the spring snow coverage and sites selected by wolverines for reproductive dens in Norway ($n = 327$) and Sweden ($n = 160$). Bars represent 95% Bonferroni-adjusted confidence intervals comparing snow cover values at den sites with proportional availability across Norway and Sweden. Confidence intervals are standardized around 1 to display preference (fully above) or avoidance (fully below). The x-axis represents the number of years out of seven (2000–2006) in which snow cover was present from 24 April to 15 May.



whether wolverine circumboreal range limits are tied to an upper limit of thermal tolerance. We compared published temperature data at 30 arc-seconds (~ 1 km) resolution for average maximum August temperatures for the years 1950–

2000 (Hijmans et al. 2005; hereafter, the summer temperature coverage) with summer wolverine telemetry data sets that represented the latitudinal gradient of wolverine occurrence.

Although the wolverine literature posits seasonal movements upward in elevation to avoid thermal stress, upper thermal limits of wolverines have not been studied (unlike reproductive denning requirements, for which we had a strong a priori hypothesis to test against observed data). Therefore, we fit temperature limits to telemetry data from eight North American and two Norwegian study areas, examined the consistency of the temperature threshold across study areas, and compared derived temperature limits with our contemporary understanding of the wolverine's current range in the Northern Hemisphere. To do so, we extracted temperature values for summer telemetry locations and created cumulative distributions of locations as a function of temperature. We chose, a priori, the 90th percentile of locations as a putative upper thermal limit for wolverines. We then created a coverage representing the spatial distribution of temperatures at or below the 90th percentile temperature value for comparison with the spring snow coverage. In addition, we extracted temperature values associated with random points within the same MCPs used to investigate selection for the spring snow coverage. These values were then used to investigate whether wolverines were selecting for areas with relatively low average summer temperatures.

Table 1. Spatial concordance between the spring snow coverage and telemetry locations from 10 wolverine study areas in North America and Scandinavia.

Study area ^a	No. of telemetry locations	Area within the spring snow coverage (%)	Telemetry locations within the spring snow coverage (%)	χ^2 critical value	χ^2 P value ^b	Seasonal telemetry locations within the spring snow coverage (%)	
						Summer	Winter
Northern Norway	1819	— ^c	— ^c	— ^c	— ^c	— ^c	— ^c
South-central Norway	455	90.7	98.1	29.7	<0.001	98.5	97.6
Omineca Mountains, British Columbia	1206	77.4	74.4	6.3	(0.011)	85.6	67.5
Revelstoke, British Columbia	2007	85.1	93.6	1919.8	<0.001	89.8	83.3
Northern Cascade Range, Washington	345	73.8	90.7	50.9	<0.001	97.6	79.3
Glacier National Park, Montana	793	81.2	93.1	73.5	<0.001	95.0	92.0
Lolo Pass, Montana and Idaho	44	60.6	79.5	6.6	0.010	83.3	83.0
Pioneer Mountains, Montana	251	46.8	74.9	79.4	<0.001	76.6	71.3
Central Idaho	983	61.4	86.8	267.8	<0.001	91.5	81.7
Greater Yellowstone Ecosystem, Wyoming, Montana, and Idaho	1846	54.6	93.6	1131.0	<0.001	95.2	92.9

^aThe geographic location of each study area is shown in Fig. 5.^bProbability values in parentheses indicate avoidance.^cThe northern Norway study area was entirely snow-covered.

97.9% (550) of the den sites occurred in pixels that were snow-covered in at least 1 of 7 years. Den-site selection relative to years with snow was similar in Norway and Sweden and indicated that Scandinavian wolverines preferred den sites that were snow-covered for 6–7 years ($\chi^2 = 259.63$, $P < 0.0001$) (Fig. 4). North American wolverines also located their dens within the spring snow coverage, and most dens (45/65; 69%) were located in areas that were snow-covered for 6–7 years. Two dens in Norway, one den in Sweden, eight dens in Finland, and one den in Ontario, Canada, fell outside the spring snow coverage. All of these den sites were investigated and determined to be snow dens; they occurred in areas where snow cover was insufficient to classify the 500 m $\times$ 500 m area as persistently snow-covered through 15 May.

For the nine telemetry study areas included in analyses of snow-cover selection (Fig. 5, excluding *i*), the spring snow coverage included 89% of the telemetry points but only 72% of the total area within MCPs (Table 1, Fig. 6). Ninety-five percent of summer locations and 86% of winter locations fell within the spring snow coverage (Table 1). In seven of eight North American study areas and in southern Norway, wolverines selected for areas within the spring snow coverage during winter, summer, and when seasons were pooled. In the Omineca Mountains study area in British Columbia (Fig. 5), wolverines avoided the spring snow coverage in winter and when seasons were pooled (Table 1), but selected for it during the summer months.

The 90% cumulative temperature value varied by 10.3 °C across the 24° of latitude encompassed by the 10 study areas (Table 2). In the more northerly study areas, higher temperatures were less available and wolverine use generally mirrored availability, although lower temperatures were preferred within most study areas (Table 2, Fig. 7). Temperature use diverged from availability between 56°N and 52°N latitude (Fig. 7). At southerly latitudes in North America, wolverines selected for cooler habitats in the summer (Table 2, Fig. 7), with 90% of telemetry locations occurring in areas with average maximum August temperatures ≤ 22 °C (averaged across all study areas south of 56°N latitude). Areas in this temperature range were much more concordant with the spring snow coverage at southerly latitudes (Table 2, Fig. 1). In North America, the spring snow coverage and maximum summer temperature models diverged from each other at about 54°N latitude, just south of the Omineca Mountains study area (Fig. 8).

The wolverine's southern range limits generally extended slightly beyond the spring snow coverage, particularly in areas with low topographic relief (Fig. 1). Areas where current range limits were not consistent with persistent spring snow cover included areas of recent extirpation (southern portions of Norway, Sweden, and Finland; Quebec, Canada; California and Colorado, US) and Eurasian regions where the historical presence of wolverines is largely unknown. These include southern montane regions, such as the Alps and the Carpathian Mountains in Europe and the Himalayas in southern Asia (Fig. S2).² The summer temperature coverage extends far south of both the current range of wolverines and the spring snow coverage, including coastal areas where maritime influences keep temperatures low (Fig. 1).

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."

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

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92

Cor-B-53

A Handbook for
Conservation
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by

David S. Dobkin

The High Desert Museum
Bend, Oregon

Cal Base-South
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CASSIN'S FINCH

Carpodacus cassinii
Fringillidae

Summer, Permanent, or Winter Resident

WINTERING AREA: 5

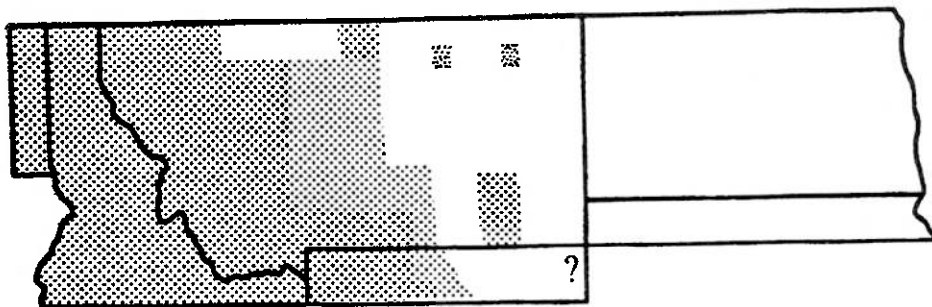
HABITAT REQUIREMENTS: Drier montane coniferous forests and woodlands, especially of ponderosa pine. Nests in coniferous trees.

FEEDING: Dines primarily on seeds of conifer trees, also takes insects, buds and berries. Forages on the ground and by gleaning from foliage in trees and shrubs.

STATUS AND MANAGEMENT: Numbers have been highly erratic in Idaho but appear to be increasing

there; numbers have been more stable in Montana but appear to be declining slightly. In the West as a whole, numbers show a small but significant increasing trend. Prefers older rotation-age stands (Mannan and Maslow, 1984) and harvest units (Moore, 1992) over old growth. Cassin's Finch is a nomadic, semi-colonial breeder with resultant fluctuations in local population numbers.

FURTHER READING: Hejl et al., 1988; Mewaldt and King, 1985; Samson, 1976.



Condor 90: 689-1988

BREEDING BIOLOGY OF THE GREAT GRAY OWL IN SOUTHEASTERN IDAHO AND NORTHWESTERN WYOMING¹

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Abstract. In this study, I documented the existence of a breeding population of Great Gray Owls (*Strix nebulosa*) in southeastern Idaho and northwestern Wyoming and recorded aspects of this species' breeding biology between 1980 and 1983. Thirty-eight pairs were found; 25 fledged young at least once. Fifteen nests were documented; 40% in old stick nests and 60% on tops of broken-top snags. Nests were frequently reused. Mean date of egg laying was 5 May. Onset of egg laying appeared to be delayed during years of higher snow depth. Mean clutch and brood sizes were 3.3 and 3.0, respectively. Seventy-one percent of the nest attempts were successful. Fledged young moved at a constant rate and direction away from the nest before they were able to fly. Northern pocket gophers (*Thomomys talpoides*) and voles (*Microtus* spp.) constituted 57.9% and 34.1% frequency of the diet, respectively. Great Gray Owls nesting near clearcuts had higher percentages of pocket gophers in their diet while those nesting near natural meadows had higher percentages of voles.

Key words: Great Gray Owl; Idaho; Wyoming; breeding biology; food habits; *Strix nebulosa*.

INTRODUCTION

The Great Gray Owl (*Strix nebulosa*) is found in the boreal climatic zones of North America and Eurasia (Mikkola 1983). The breeding range in North America is from central Alaska and Canada, south to central California, the northern Rocky Mountains, extreme northwestern Minnesota and south-central Ontario (Collins 1980, Nero 1980). Idaho and Wyoming were included in the breeding range of this species based on four records of young (Hand 1941, Johnson 1974, Collins 1980) and one nest (Craighead and Craighead 1969) observed between 1931 and 1975. In addition, 17 specimens and 12 sight records collected between 1906 and 1974 provided additional, if limited, information on the occurrence of Great Gray Owls in Idaho and Wyoming (Kemsies 1935, Bent 1938, Long 1941, Test 1941, Scott 1970, Collins 1980).

The breeding biology of Great Gray Owls has been summarized by Collins (1980) and Nero (1980) for Canada, and by Mikkola (1983) for Eurasia. However, few studies have been conducted on Great Gray Owls in the southern portion of their range in the continental United States (Winter 1979, 1981, 1982a, 1982b; Evelyn Bull, pers. comm.).

In this study, I documented a breeding pop-

ulation of Great Gray Owls in southeastern Idaho and northwestern Wyoming and recorded aspects of this species' breeding biology between 1980 and 1983.

METHODS

The study area encompassed about 24,000 km² in northwestern Wyoming and southeastern Idaho and included the Targhee National Forest (TNF), the Teton portion of the Bridger-Teton National Forest (BTNF), Grand Teton National Park (GTNP), and Yellowstone National Park (YNP) (Fig. 1). The study area was described in more detail by Franklin (1987).

Locations of Great Gray Owls within the study area were initially collected from unpublished records from the TNF, BTNF, YNP, and GTNP. Between April and August of 1980 through 1982, areas of historic observations were searched during the day for nests and surveyed during the night using broadcasted territorial calls from an 8-W cassette tape player. A limited amount of data was collected in August 1983. Surveys were used only to locate nesting pairs within the study area. The study area was not systematically censused to obtain estimates of abundance or density.

Monthly snow depths for January through May were obtained annually from 40 snow course stations (U.S. Dep. Agric. Soil Conserv. Serv.) distributed at different elevations throughout the study area.

¹ Received 20 January 1988. Final acceptance 12 April 1988.

Condor 90: 1988

Snag dbh
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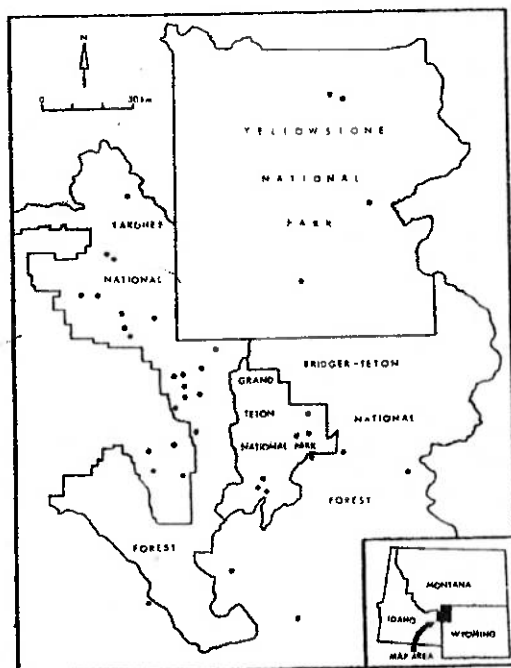


FIGURE 1. Map of the study area in southeastern Idaho and northwestern Wyoming showing locations of Great Gray Owl pairs (dots).

Time-lapse cameras were installed at three nests in 1981 and five nests in 1982 to record nesting chronology. Time-lapse cameras consisted of Minolta Autopack D6 movie cameras housed in waterproof aluminum cases. Telonics TIC-2 intervalometers were used to expose one frame of Ektachrome 160 Super 8 mm movie film every 3 min during the day. Cameras were installed above the nest in trees about 15 to 20 m from the nest. All nests were checked every 3 to 5 days by climbing trees adjacent to the nest to count eggs and young in the nests. Females usually left the nests and perched nearby during these climbs but returned to the nest within 5 min. No mortality of eggs or young was attributed to nest-site visits.

Movements from the nest and roost locations of young were documented every 3 to 5 days by searching the area surrounding the nest. At each roost location used by young, I measured the distance and direction from the nest with a compass and tape measure and the height of the young above the ground with a clinometer. Fifty-eight directions from nests to roosts of young were pooled for each nest and analyzed using circular statistics (Batschelet 1981).

Nest trees were measured after the young left the nest. At each nest tree, I measured the following variables: (1) nest height, with a clinometer, (2) diameter at breast height (DBH) of the nest tree, with a diameter tape, and (3) the surface area available for nesting, by two taped measurements across the nest surface and using the formula for computing the area of either a circle or an ellipse.

Meadow and clearcut cover-types within a 2.59-km² circle centered around nests were considered potential foraging habitat (Winter 1982a, Mikkola 1983). A 2.59-km² circle approximated the home range for Great Gray Owls (Craighead and Craighead 1969, Winter 1982a). Cover-types within the circle were outlined on aerial photographs (scale = 1:15,840) and their areas measured with a polar planimeter. Clearcuts were defined as logged areas, and meadows as natural openings. I computed a clearcut index, expressed as a percentage, by dividing the area of clearcut within the potential foraging habitat around each nest by the total area of clearcut and meadow within the potential foraging habitat.

I determined the composition of prey taken by Great Gray Owls by collecting regurgitated pellets around nests and under roost sites of young and adults. Each nest was considered a separate sampling location. Prey items were identified to species using skull characteristics (Glass 1973, Larrison and Johnson 1981). Biomass was approximated for each prey species using mean weights in Burt and Grossenheider (1964), Forsman (1975), and Weaver (1977). Skulls of northern pocket gophers (*Thomomys talpoides*) were classified as juveniles or adults based on lengths of upper and lower incisor bevels and molariform rows using criteria in Weaver (1977) and Franklin (1987). At each nest where pellets were collected, I computed a *Thomomys* index, expressed as a percentage, by dividing the frequency of *Thomomys* in the diet by the total frequency of *Thomomys* and *Microtus* in the diet.

Nonparametric tests were used for pairwise comparisons and bivariate associations (Daniel 1978, Sokal and Rohlf 1981). Tests of independence and homogeneity were evaluated using chi-square (Sokal and Rohlf 1981).

RESULTS

DISTRIBUTION AND ABUNDANCE

I recorded 255 sightings of Great Gray Owls within the study area. Most (67.5%) of the sight-

TABLE 1. Measures of Great Gray Owl nesting success in Wyoming. Data are from 1981 and 1982.

Nest type ^a
LPP snag
DF/ES snag
All snag
Stick
Overall

^a LPP = lodgepole pine, DF/ES = Douglas-fir/Engelmann spruce.

ings were from 10 ring after 1960. Sixty-one (23.5%) of the nests where active observed was 2,000 to 3,000 m above the ground. Ninety percent of the sightings were in lodgepole pine (*Pinus contorta*)/Douglas-fir (*Pseudotsuga*)/aspen (*Populus*) included the lower area.

Thirty-eight pairs of Great Gray Owls were active between 1981 and 1982. Five of the pairs were active in 1981 and 33 in 1982. Twenty-five (65%) of the pairs were known to have a mean of 7.2 young per pair. GTNP had been active in 1947 and 1983 (3 pairs in 1947 and 1981).

NEST SITES

Fifteen nests have been active since 1947 (one in 1947, one in 1973, one in 1977, one in 1978, one in 1979, one in 1980, one in 1981, one in 1982, one in 1983, one in 1984, one in 1985, one in 1986, one in 1987, one in 1988, one in 1989).

Nine (60%) of the nests were on the tops of trees. These were in lodgepole pine, Douglas-fir, and aspen. Six (40%) of the nests were on the ground and in shrubs. Six (40%) of the nests were in aspen, and one in Douglas-fir.

Nests in lodgepole pine were the ground and in shrubs (Table 1). Stick nests (largest surface area combined) were six

TABLE 1. Measurements of nests and nest trees of Great Gray Owls in southeastern Idaho and northwestern Wyoming. Data are $\bar{x} \pm SD$ with n in parentheses.

Nest type ^a	Height of nest aboveground (m)	DBH ^b of nest tree (cm)	Nesting surface area (cm ²)
LPP snag	4.0 $\pm$ 0.3 (3)	50.8 $\pm$ 6.7 (3)	808 $\pm$ 217 (3)
DF/ES snag	7.5 $\pm$ 1.1 (4)	71.8 $\pm$ 13.8 (4)	1,172 $\pm$ 381 (3)
All snag	6.0 $\pm$ 2.0 (7)	62.8 $\pm$ 15.3 (7)	990 $\pm$ 342 (6)
Stick	11.1 $\pm$ 2.7 (5)	38.6 $\pm$ 17.5 (5)	2,445 $\pm$ 281 (5)
Overall	8.1 $\pm$ 3.4 (12)	52.7 $\pm$ 19.9 (12)	1,651 $\pm$ 817 (11)

^a LPP = lodgepole pine, DF/ES = Douglas-fir/Engelmann spruce.

^b Diameter at breast height.

ings were from 1980 to 1983 with 94.1% occurring after 1960. Sightings were recorded between 1,524 and 3,000 m elevation. The mean elevation where active nests and fledged young were observed was 2,078 m ($SD = 241$, $n = 41$). Over 90% of the sightings were in the lodgepole pine (*Pinus contorta*)/Douglas-fir (*Pseudotsuga menziesii*)/aspen (*Populus tremuloides*) zone which included the lower half of the forested slopes in the area.

Thirty-eight pairs were found within the study area between 1980 and 1983 (Fig. 1). Twenty-five of the pairs were reproductively active, fledging young at least once during the 4-year study period. Twenty-four areas (defined by 2.59-km² circles) were known to be occupied by pairs for a mean of 7.2 years ($SD = 8.4$). One area in GTNP had been sporadically occupied between 1947 and 1983 (36 years) with young fledged in 1947 and 1981.

NEST SITES

Fifteen nests have been found in the study area; one in 1947 (Craighead and Craighead 1969), one in 1973 (D. Taylor, pers. comm.), three in 1977 (C. Youmans, pers. comm.; E. Bowman, pers. comm.), one in 1979 (T. Weaver, pers. comm.), and nine during this study.

Nine (60%) of the nests were in shallow depressions on the tops of broken-top snags. Five of these were in lodgepole pine snags, three in Douglas-fir snags and one in an Engelmann spruce (*Picea engelmannii*) snag. All of the snags were in advanced stages of decay (sensu Cline et al. 1980). Six (40%) of the nests were in old stick nests; four were in lodgepole pines, one in an aspen, and one in a Douglas-fir snag.

Nests in lodgepole pine snags were lower to the ground and had the smallest surface area (Table 1). Stick nests were the highest and had the largest surface area. Nests in snags (all tree species combined) were significantly closer to the ground

(Mann-Whitney U -test, $U = 33$, $P < 0.05$), in trees of larger DBH ($U = 30$, $P < 0.05$), and had smaller surface areas ($U = 30$, $P < 0.01$) than stick nests.

Nest destruction over 2 years appeared greatest in lodgepole pine snags followed by stick nests. Two lodgepole pine snags used for nesting were felled during a windstorm while a third was depredated. Two stick nests were destroyed by wind. I observed no loss of nests in Douglas-fir/Engelmann spruce snags.

Five nests observed over a 2-year period (one nest in 1947–1948, F. Craighead, pers. comm.; two nests in 1977–1978, C. Youmans, pers. comm.; two nests in 1981–1982, this study) were occupied each year and were reproductively successful. A sixth nest was used for four consecutive years (1980 to 1984), producing two to three young each year. A seventh nest was active in 1980, 1981, and 1983, but not in 1982. In 1982, time-lapse films recorded an adult on this nest

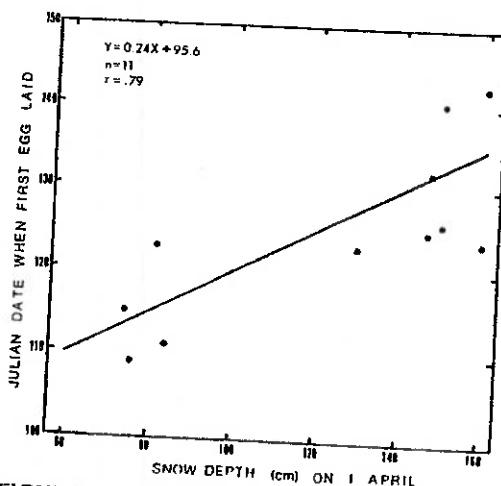


FIGURE 2. Julian date of first egg laid in relation to snow depth on 1 April at Great Gray Owl nests in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.01$.

Handwritten notes on the right margin:
 $DF = \frac{71.8}{2.54} = 28.2$
 $LPP = \frac{50.8}{2.54} = 20.0$

TABLE 2. Reproductive output of Great Gray Owls in southeastern Idaho and northwestern Wyoming.

	Observed frequency of n^* individuals				$\bar{x}$	SD	n
	1	2	3	4			
Clutch size	0	2	2	4	3.3	0.3	8
Brood size	1	2	6	4	3.0	0.3	13
Size of fledgling groups ^a	1	0	4	2	3.0	0.4	7
Size of fledgling groups able to fly	1	3	1	0	2.0	0.3	5

* n = number of eggs for clutch size and number of young for the other three variables.

^a Not yet capable of flight.

for 15 to 20 min on 27 April and 1 May with no other activity recorded for the rest of the year.

NESTING CHRONOLOGY

Before egg laying, adults were frequently recorded at the nest. Time-lapse photography at two nests revealed that adults repeatedly visited the nests 17 to 25 days before the females settled on the nest. One or both of the owls made at least one to four trips daily to the nest ($\bar{x} = 2.3$, $SD = 1.0$, $n = 19$) each or every other day and spent 3 to 75 min at the nest ($\bar{x} = 15$, $SD = 16$, $n = 42$) during daylight visits.

The mean date when the first egg was laid was 5 May ($SD = 9.9$ days, $n = 11$). The date when the first egg was laid was significantly correlated with snow depth at the onset of the breeding season (defined as 1 April) (Fig. 2). Eggs were laid as early as 19 April under conditions of relatively shallow snow and as late as 23 May when snow was deeper.

Incubation period (from the laying of the first egg to the hatching of the last egg) averaged 29.7 days ($SD = 1.6$, $n = 3$ clutches). Young left their nests at a mean age of 28.5 days ($SD = 1.5$, $n = 6$). At this stage, the young were considered fledged even though they were incapable of flight. Young were capable of sustained gliding flight an average of 14.2 days ($SD = 1.1$, $n = 5$) after leaving the nest.

REPRODUCTIVE OUTPUT

The most common clutch was three to four eggs (75.0%) and the most common brood was three to four young (76.9%) (Table 2). Annual clutch size ranged from a mean of 3.0 ($n = 4$) in 1981 to 3.3 ($n = 4$) in 1982. Clutch sizes in this study were not statistically different (Mann-Whitney U -test, $U = 110-149$, $P > 0.50$) from clutch sizes from two other studies in North America (Oeming 1955 [$n = 23$ clutches], Collins 1980 [$n = 11$]). However, comparison of the pooled data from North America with data from four studies

($n = 21, 28, 30$, and 66 clutches) in Finland and Sweden (Hildén and Helo 1981), which also were not significantly different (Mann-Whitney U -test, $U = 380-898$, $P > 0.12$), revealed that clutch sizes in North America ($\bar{x} = 3.2$, $n = 34$) were significantly smaller (Mann-Whitney U -test, $U = 3,709$, $P < 0.001$) than clutch sizes in Scandinavia ($\bar{x} = 4.3$, $n = 145$).

Between 1980 and 1983, eggs were laid in 88.2% of 17 nesting attempts while young were fledged in 70.5% of the attempts. Nests in lodgepole pine snags, stick nests and fir/spruce snags averaged 1.0 ($n = 4$), 3.0 ($n = 4$), and 3.3 ($n = 4$) fledglings per nesting attempt, respectively. The annual number of fledglings per successful nest, or productivity, ranged from a mean of 2.7 ($n = 3$) in 1981 to 3.0 ($n = 3$) in 1982.

Survival probabilities for young were determined at eight nests where eggs and young were followed through most or all of the developmental stages. A young Great Gray Owl had a probability of 0.76 ($n = 25$) of surviving incubation as an egg, 0.89 of surviving as a nestling ($n = 19$), and 0.77 of surviving through the flightless stage after fledging ($n = 13$).

MOVEMENTS OF FLEDGLINGS

Eleven banded young, fledged from five nests, moved at a constant rate (Fig. 3) and in a constant direction ($n = 58$ directions measured) away from the nest as they grew older. Mean directions taken by family groups were roughly north ($n = 2$; 19° and 32°), south ($n = 1$; 176°), and southwest ($n = 2$; 224° and 250°). The r values for the mean directions were high (range = 0.83–0.96) and significantly directed (Rayleigh test, $P < 0.001$) indicating that each family group maintained a constant compass direction as they moved away from the nest.

The height which fledglings roosted above the ground was significantly correlated with the age of the fledglings (Fig. 4). The roost sites used by fledglings as they moved away from their nests,

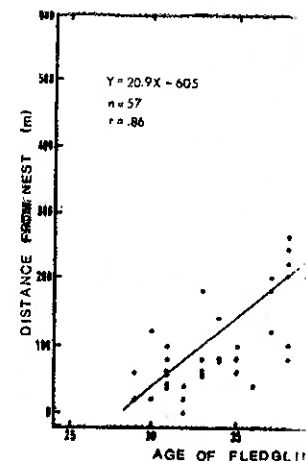


FIGURE 3. Distances moved by Great Gray Owls in relation to the age of the fledglings. The correlation coefficient is significant.

but before they could fly, were categorized (Fig. 5); (1) most accessible ($n = 8$), (2) moderately accessible ($n = 31$), and (3) least accessible ($n = 31$). Using the three categories of accessibility, the results were significantly different (Mann-Whitney U -test, $P < 0.05$). Accessibility was determined by the ease with which the fledglings reached by mammalian predators, a direct function of accessibility.

FOOD HABITS

Northern pocket gophers and constituted 92.0% (by frequency) of 435 prey items identified from 65.8% from pellets collected at eight nests (Table 1). Gopher skulls aged, 76.4% were collected in July ($n = 22$), and 8.8% in August ($n = 8$).

Comparisons of the frequency of prey placed in three categories (Threat, Other, and "Other" prey) resulted in no significant differences between containing nests not significantly different from each other. Nest group A ($\chi^2 > 0.10$) included five nests ($n = 7$), group B ($\chi^2 = 4.8$, $df = 2$) included two nests ($n = 72$ prey) which contained 3.0 young ($n = 2$), and group C ($\chi^2 = 2$, $P > 0.05$) included two nests.

egg lay = ap 19 → May 23
 egg hatch = May 19 → June 22 (30 day incubation)
 Fledge (28.5 days) = June 17 → July 21

Fly at 14.2 days = July 3 → August 4

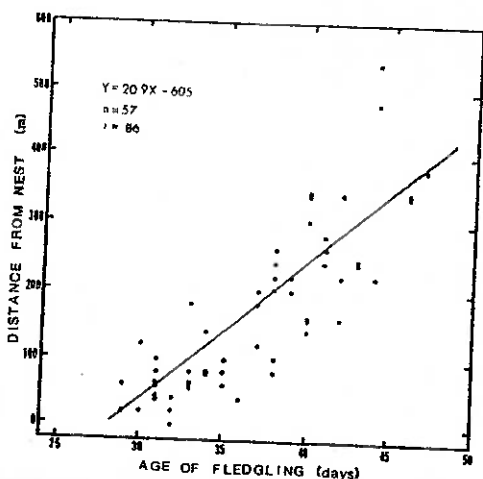


FIGURE 3. Distances moved from nests by fledgling Great Gray Owls in relation to their age in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.001$.

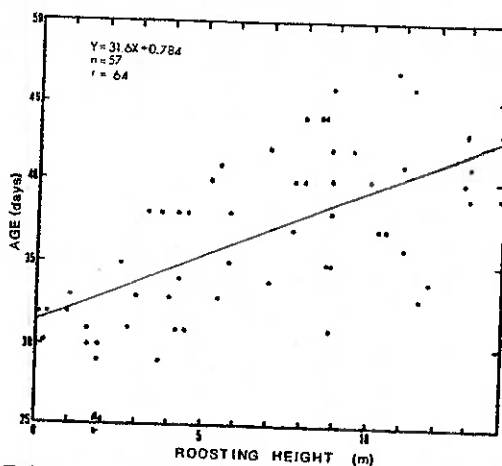


FIGURE 4. Height at which fledgling Great Gray Owls roosted in relation to their age in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.001$.

but before they could fly, were assigned to three categories (Fig. 5); (1) most accessible to the young ($n = 8$), (2) moderately accessible ($n = 18$), and (3) least accessible ($n = 31$). Mean age of young using the three categories of roosts differed significantly (Mann-Whitney U -test, $U = 112-433$, $P < 0.05$). Accessibility was subjectively determined by the ease with which roosts could be reached by fledglings that could not fly. Vulnerability to mammalian predators was considered a direct function of accessibility.

FOOD HABITS

Northern pocket gophers and *Microtus* spp. constituted 92.0% (by frequency) and 92.9% (by biomass) of 435 prey items identified from pellets collected at eight nests (Table 3). Of 72 pocket gopher skulls aged, 76.4% were from juveniles; 65.8% from pellets collected in June ($n = 38$), 90.9% in July ($n = 22$), and 87.8% in August ($n = 8$).

Comparisons of the frequency of prey items placed in three categories (*Thomomys*, *Microtus*, and "Other" prey) resulted in three nest groups, containing nests not significantly different from each other. Nest group A ($\chi^2 = 13.0$, $df = 8$, $P > 0.10$) included five nests ($n = 199$ prey items) which fledged a mean of 2.9 young ($SD = 1.1$, $n = 7$), group B ($\chi^2 = 4.8$, $df = 2$, $P > 0.05$) included two nests ($n = 72$ prey) which fledged an average of 3.0 young ($n = 2$), and group C ($\chi^2 = 4.1$, $df = 2$, $P > 0.05$) included two nests ($n = 160$ prey)

where the reproductive outcome was unknown. Differences in frequencies of *Thomomys* and *Microtus* among all three nest groups were significant ($\chi^2 = 4.3-92.3$, $df = 1$, $P < 0.05$) but not significant in the Other category ($\chi^2 = 0.1-1.2$, $df = 1$, $P > 0.25$). Percentages of *Thomomys* in the diet decreased, as *Microtus* increased, in groups A, B, and C, respectively (Fig. 6).

The differences in occurrence of prey may be partially explained by the types of foraging habitat around the nests. The amount of *Thomomys* in the diet appeared directly proportional to the amount of clearcut surrounding the nests (Fig. 7).

DISCUSSION

Productivity in this study was high with a mean of 3.0 young fledged per successful nest as com-

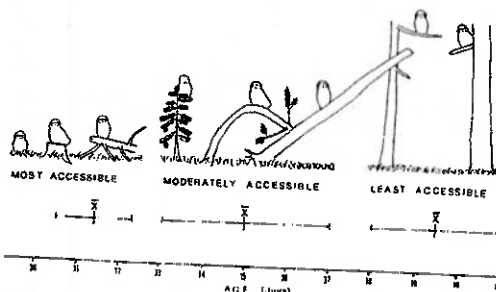


FIGURE 5. Mean age of fledgling Great Gray Owls using three categories of roosts in southeastern Idaho and northwestern Wyoming. Values represent means $\pm$ 95% confidence intervals around the mean.

TABLE 3. Prey items found in Great Gray Owl pellets in southeastern Idaho and northwestern Wyoming.

Prey species	n	Frequency (%)	Biomass (g)	Biomass (%)
<i>Thomomys talpoides</i>	252	57.9	17,415	69.4
<i>Microtus montanus</i>	139	32.0	3,560	22.1
<i>Microtus agrestis</i>	2	0.5	80	0.3
<i>Microtus richardsoni</i>	7	1.6	280	1.1
<i>Peromyscus maniculatus</i>	7	1.6	154	0.6
<i>Sorex</i> spp.	6	1.4	60	0.2
<i>Tamiasciurus hudsonicus</i>	3	0.7	600	2.4
<i>Clethrionomys gapperi</i>	3	0.7	75	0.3
<i>Zapus princeps</i>	3	0.7	90	0.4
<i>Onychomys leucogaster</i>	3	0.7	90	0.4
Unidentified bird	10	2.2	700	2.8
Total	435	100.0	25,104	100.0

pared to 2.3 in Oregon (Evelyn Bull, pers. comm.) and 2.7 to 3.9 in Finland and Sweden (Hildén and Helo 1981). Nesting success in this study was also high and similar to that observed in Oregon (75%, Evelyn Bull, pers. comm.). Despite larger clutches in Finland, the average number of fledglings per nest attempt ($\bar{x} = 2.4$, $n = 42$) in Finland (Mikkola 1981) was similar to that found in this study because of lower nestling survival in Finland than in this study (72% vs. 89%, respectively). Hatching rates were similar (81% in Finland and 76% in this study).

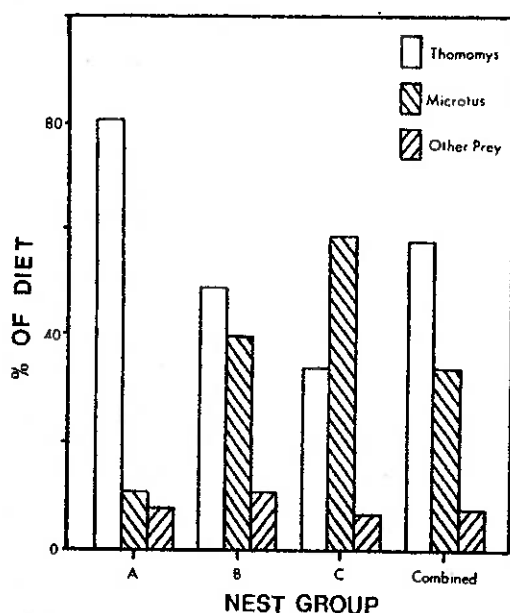


FIGURE 6. Percent of three prey categories in three groups of Great Gray Owl nests in southeastern Idaho and northwestern Wyoming. Prey categories and nest groups are explained in the text.

In this study, nests in fir/spruce snags were more productive and stable than nests in lodgepole pine snags and stick nests. Those in fir/spruce snags (1) had a larger nesting surface area, (2) were taller and, therefore, relatively inaccessible to predators, and (3) were more durable.

Great Gray Owls in North America use different proportions of stick nests and broken-top snags for nesting within different parts of their geographic range. In order of decreasing latitude, the ratio of snag to stick nests average 1:20 ($n = 42$) in Canada and Minnesota (Roberts 1936; Robinson 1954; Oeming 1955; Parmelee 1968; Nero 1970, 1984; Muir 1972; Kondla 1973; James 1977; Eckert 1979; Collins 1980; Houston and Wylie 1984), 1:2.5 ($n = 41$) in Oregon (Evelyn Bull, pers. comm.), 1:0.7 ($n = 15$) in this

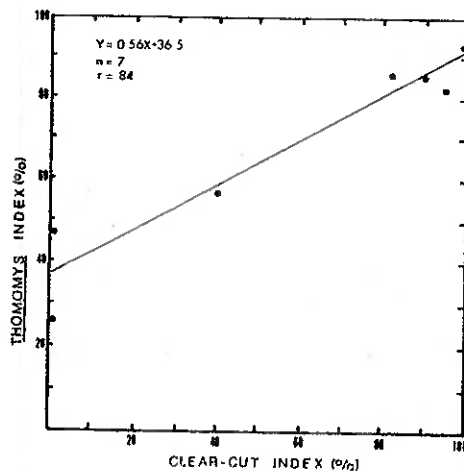


FIGURE 7. *Thomomys* index in relation to clearcut index at seven nests in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.03$.

study and 1:0 ($n = 8$) in 1982a). Use of snags is times more common in and northern Finland of snags as nests may be able within different breeding range.

After leaving the nest perches near the nest predators (Oeming 1968; Nero 1970, 1977; Follen 1979; C fledged young probably ability of roosts such trees which are accessible allows them to roost high predators and (2) the within a 500-m radius reason for the unidirectional group is unknown dictable. However, No male using vocalization the nest indicating th may be controlled by t

During the breeding prey in Great Gray Owl ada was in the family M Hoglund and Langsgrö kola and Sulkava 197 Pulliainen and Loisa 19 phers (*Thomomys* spp. of the diet of Great G part of their range in Bull, pers. comm.; Wi Therefore, pocket goph important prey for Great G portion of their North

In this study, Great clearcuts may be utilized small mammal species and Teipner et al. (1981) sites of pocket gophers other habitats. In addition phers were present in the ages than were typically ture of northern pocket proportion of juvenile goph Youmans (1979) was 7 and 78% in August as and 88% juvenile gophers Gray Owls in this study respectively. Great Gray most vulnerable age class

study and 1:0 ($n = 8$) in California (Winter 1980, 1982a). Use of snags for nests is almost three times more common in southern than in central and northern Finland (Mikkola 1983). The use of snags as nests may be related to nest-site availability within different proportions of this species' breeding range.

After leaving the nest, young climbed available perches near the nest probably to escape ground predators (Oeming 1955; Hoglund and Langsgren 1968; Nero 1970, 1984; Pulliainen and Loisa 1977; Follen 1979; Collins 1980). Survival of fledged young probably depends on: (1) the availability of roosts such as leaning and deformed trees which are accessible to them and which allows them to roost high enough to avoid ground predators and (2) the existence of forested habitat within a 500-m radius surrounding the nest. The reason for the unidirectional movements by family groups is unknown and appears to be unpredictable. However, Nero (1980) observed a female using vocalizations to lure young away from the nest indicating that movements by young may be controlled by their parents.

During the breeding season, over 90% of the prey in Great Gray Owl diets in Europe and Canada was in the family Microtidae (Oeming 1955; Hoglund and Langsgren 1968; Nero 1969; Mikkola and Sulkava 1970; Mikkola 1972, 1981; Pulliainen and Loisa 1977). However, pocket gophers (*Thomomys* spp.) constituted 34 to 58% of the diet of Great Gray Owls in the southern part of their range in North America (Evelyn Bull, pers. comm.; Winter 1982a; this study). Therefore, pocket gophers appear to be an important prey for Great Gray Owls in the southern portion of their North American range.

In this study, Great Gray Owls nesting near clearcuts may be utilizing the most abundant small mammal species available. Barnes (1973) and Teipner et al. (1983) reported higher densities of pocket gophers in clearcut areas than in other habitats. In addition, juvenile pocket gophers were present in the diet in higher percentages than were typically present in the age structure of northern pocket gopher populations. The proportion of juvenile gophers found in YNP by Youmans (1979) was 7% in June, 39% in July, and 78% in August as compared to 66%, 91%, and 88% juvenile gophers in the diet of Great Gray Owls in this study during those months, respectively. Great Gray Owls may be taking the most vulnerable age class of this prey since young

pocket gophers often disperse aboveground (Chase et al. 1982). Winter (1982a) suggested that reduced microtine abundance could severely limit reproduction by Great Gray Owls. In this study, however, fledgling success was high at nests where high percentages of pocket gophers were present in the diet.

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**HABITAT USE BY
THREE-TOED AND BLACK-BACKED WOODPECKERS,
DESCHUTES NATIONAL FOREST, OREGON**

by
Rebecca Goggans, Rita D. Dixon, and L. Claire Seminara

Nongame Project Number 87-3-02
Oregon Department of Fish and Wildlife
U.S.D.A. Deschutes National Forest

ABSTRACT

Patterns of habitat use for home ranges, foraging, nesting, and roosting, were described for three-toed (Picoides tridactylus) and black-backed (Picoides arcticus) woodpeckers on the Deschutes National Forest, Oregon, during April-September, 1986 and 1987. A severe mountain pine beetle epidemic had created an abundance of dead and dying trees, and an aggressive pest management and timber salvage program had created a patchwork of logged areas, primarily shelterwood cuts, on the study area.

All nests excavated by three-toed and black-backed woodpeckers were in portions of lodgepole pine (Pinus contorta) trees with heartrot. Evidently, both species require soft wood for excavating cavities, because of morphological adaptations associated with 3 toes on each foot. Habitat selection for mature and overmature forest stands, and against younger stands and logged areas, was documented for three-toed woodpeckers using 16 nests, 493 forage bouts, and 16 roosts, and for black-backed woodpeckers using 35 nests, 395 forage bouts, and 20 roosts. Home range sizes for 3 radio-tagged three-toed woodpeckers were 751, 351, and 131 acres (n=170, 352, and 131 locations, respectively). Home range sizes for 3 radio-tagged black-backed woodpeckers were 810, 303, and 178 acres (n= 124, 86 and 112 locations, respectively). Intra-specific home range overlap among both species appeared limited or nonexistent, except among paired individuals near the nest site. Inter-specific home range overlap was common between three-toed and black-backed woodpeckers and other Picidae.

Guidelines for management included establishing Management Areas which retain the characteristics of mature and overmature lodgepole pine or lodgepole pine-mixed conifer forest stands. Recommended sizes of Management Areas were 528 acres per pair of three-toed woodpeckers, at a minimum elevation of 4500 ft, and 956 acres per pair of black-backed woodpeckers, with some Areas at elevations less than 4500 ft. One Management Area could be designated for both species, if the respective habitat needs were met.

SUMMARY

INTRODUCTION

Three-toed and black-backed woodpeckers are two of the least known species of woodpeckers in North America. They are sympatric over most of their North American range and both are nonmigratory residents on the east slope of the Cascade Mountain Range. The woodpeckers are associated with trees characterized by scaly or flaky bark, but differ in the species of trees with which they are associated; the three-toed woodpecker is more closely associated with spruce (Picea spp.), and the

roosts were on the lower study area where only lodgepole pine forest type was available. Mean canopy closure at roost sites was 40%. Mean dbh of trees in the roost stand was 6.0 in. Mean basal area of roost stands was 115 ft²/acre. Lodgepole pine trees were used for 14 roosts. Mean dbh of roost trees was 11.0 in. Mean tree height was 65 ft.

MANAGEMENT IMPLICATIONS

Mature and overmature forest stands have a high incidence of disease, decay and mortality. Trees with disease and decay are undesirable components of a managed forest, but were used by three-toed and black-backed woodpeckers for home range, nesting, roosting, and foraging habitat. Nests were excavated in trees with heartrot, roosts were in diseased portions of trees or decayed snags, and forage sites were in mature and overmature stands, which have abundant disease and decay, and consequently abundant wood-boring insects. Conversion to and maintenance of lodgepole pine and lodgepole pine-dominated mixed conifer stands in a young, vigorous condition may eliminate or severely restrict incidence of wood-boring insects and heartrot, leading to declines in populations of three-toed and black-backed woodpecker. ☆

Acreage of mature and overmature lodgepole pine forest stands are declining throughout the Oregon Cascades, because these stands are the prime target of the mountain pine beetle. Stands which experience high mortality nonetheless provide habitat for three-toed and black-backed woodpeckers. Individual trees within a stand may remain standing 10, 15 or 20 years, thus providing a continuum of habitat.

Treating these stands, by logging, immediately converts them to a vigorous condition where incidence of death and decay is severely restricted, thus potential nesting and foraging substrate is drastically reduced. Although in time, stands without treatment may be structurally similar to treated stands, the time to reach that condition differs significantly. Because stands without treatment continue to provide habitat over a longer time than treated stands, thus there is a shorter period when old growth lodgepole pine is absent or scarce on the Deschutes or other National Forests. Consequently, a larger population of woodpeckers may survive,

thereby increasing the potential for maintaining viable populations of both species.

Designation of the three-toed woodpecker as an Indicator Species for mature and old growth lodgepole pine appeared appropriate, but only at elevations greater than 4500 ft. Much of the pure lodgepole pine on the east slope of the Cascade Mountain Range in Oregon occurs at elevations less than 4500 ft. We recommended the black-backed woodpecker as an Indicator Species for mature and old growth lodgepole pine, instead of the three-toed woodpecker. Unlike the three-toed woodpecker, the black-backed woodpecker used a range of elevations coincident with lodgepole pine. Further, it responded to play-back recordings more frequently, over a longer time period, and with louder vocalizations than the three-toed woodpecker, thus may be more effectively monitored than the three-toed woodpecker.

Until more information is available, we believe the most effective method of insuring habitat for three-toed and black-backed woodpeckers is to exempt areas (i.e. Woodpecker Management Areas) from commercial or salvage timber management and place these areas under a special management strategy, which retains the characteristics of mature or overmature lodgepole pine habitat as long as possible, without treatment. Woodpecker Management Areas should be in lodgepole pine or lodgepole pine-dominated stands with the greatest probability of surviving the longest time, but if these stands no longer retain the characteristics of mature and overmature stands, or if the number of trees remaining is inadequate to support a pair of woodpeckers, then the designated Woodpecker Management Area should be relocated to a selected replacement. Replacement stands should be selected now, to provide the earliest possible replacement for declining Woodpecker Management Areas. Woodpecker Management Areas, and replacement areas, may be within areas previously designated as protected, such as old-growth areas, Spotted Owl Habitat Areas, winter recreation sites, Research Natural Areas, etc. Management Areas for each pair of three-toed woodpeckers should be 528 acres of lodgepole pine or mixed conifer forest in mature and overmature condition and at an elevation of 4500 ft or higher. Management Areas for each pair of black-backed woodpeckers should be 956 acres of lodgepole pine or lodgepole pine-dominated mixed conifer forest in mature and overmature condition. One Management Area of 956 acres, at an elevation of

4500 ft or higher, could be designated for 1 pair of both species. However, Management Areas for black-backed woodpeckers should not be restricted to elevations greater than 4500 ft because this species may be better adapted to conditions at lower elevations.

Black-backed woodpeckers are not currently assigned a special status (e.g. *no harvest* Indicator Species), thus designation of Woodpecker Management Areas may not be practical at this time. An alternative management strategy can be applied on a sale-by-sale basis. On each sale, habitat can be preserved for each pair of black-backed woodpeckers by removing 956 acres of inter-connected blocks of mature/overmature habitat from harvest. For example, if a sale area is 9500 acres of mature or overmature lodgepole pine-dominated habitat, management at 60% of ⁵⁷⁰⁰ potential would be for 6 pairs, or 6 areas of 950 acres each. *2650* The traditional approach for management of cavity-nesters at 60% of potential by retaining 60% of the snags and live replacement tree may be ineffective for black-backed and three-toed woodpeckers for two reasons. One - snags provide more than nesting habitat; snag retention at the 60% level is unlikely to occur in sufficient amounts to provide adequate feeding substrate for species dependent on wood-boring insects associated with trees with flaky/scaly bark. Two - this approach addresses a singular, albeit a key, component of the species' habitat. The interrelationships of an old growth, or mature/overmature ecosystem, and the species associated with it, are little known, but likely complex. Land managers do not, at this time, have the information necessary to manipulate habitat and insure these interrelationships will be maintained.

The figures for home range sizes and the amount of mature or overmature stands used by woodpeckers were estimated under conditions of abundant food supply. As the mountain pine beetle epidemic runs its course, and prey abundance declines, it is likely that the amount of area required to support a pair of three-toed or black-backed woodpecker will increase.

Three-toed and black-backed woodpeckers should be monitored to track changes in population levels as the mountain pine beetle epidemic runs its course and as the forest becomes increasingly managed, resulting in reduced levels of disease and decay. Survey routes to document number of woodpecker responses

should be monitored annually. Population levels of three-toed and black-backed woodpeckers prior to the mountain pine beetle epidemic were undocumented, thus the effects of the mountain pine beetle epidemic on population levels is unknown. A review of population irruptions by three-toed and black-backed woodpeckers in eastern North America suggested that numbers of black-backed woodpeckers increase with increasing prey abundance, but that populations of three-toed woodpeckers are much less responsive to changes in prey abundance. It is possible that numbers of black-backed woodpeckers increased as the density of mountain pine beetles increased on the Deschutes National Forest. Similarly, populations may decline as the epidemic runs its course and prey for the woodpeckers becomes scarcer. It may be difficult to distinguish between the effects of the epidemic, and of timber management to control the epidemic, on populations of black-backed and three-toed woodpeckers. Documenting breeding success in Management Areas may be an effective method of combatting public outcry if woodpecker populations decline on the Forest.

This study provides a preliminary data base on habitat use by three-toed and black-backed woodpeckers; it is intended as a springboard for other studies. The pioneering nature of the study required a limited time frame, geographic scope, and sample size. Consequently, management recommendations represent the best available information at this point in time, but are intended to evolve as more information becomes available. Additional research should be a priority for land managers. Research needs include: (1) information on habitat use in areas without a bark beetle epidemic, (2) estimates for home range sizes of individuals of both species under a range of conditions, (3) estimates for breeding home range sizes of both species, (4) information on flexibility of the species to adjust to managed forest habitat, (5) information on the relationship of habitat quality and fragmentation to home range size, and (6) information on juvenile dispersal.

Effects of Logging Pattern and Intensity on Squirrel Demography

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ABSTRACT We examined the effect of harvesting intensity and pattern on red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), and yellow-pine chipmunks (*Tamias amoenus*) in mature inland Douglas-fir (*Pseudotsuga menziesii glauca*) forests in south-central British Columbia, Canada. We sampled squirrels 1 year before harvesting through 4 years after harvesting and estimated population parameters using open-population models. Relative to unharvested stands, each of the 3 species showed a strong response to tree removal. From 2 years to 4 years after logging, red squirrel density was 40% (SE = 7.1) lower in stands with 50% basal-area tree removal. From 1 year and up to 4 years after logging, northern flying squirrel density averaged 60% (SE = 5.2) lower in harvested treatments regardless of intensity or pattern of logging. In contrast, density of yellow-pine chipmunks increased markedly with increased logging intensity. Beginning 3 years after logging, yellow-pine chipmunk density was 734% (SE = 269) greater in stands with 50% basal-area tree removal. In the short term, harvesting intensity was a more important determinant of squirrel density than harvesting pattern. Retaining > 10 m² per ha of live residual stand structure in mature inland Douglas-fir forests maintained habitat for forest-dependent species such as red squirrels and northern flying squirrels, albeit at lower densities. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2655–2663; 2007)

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KEY WORDS British Columbia, demography, Douglas-fir, *Glaucomys sabrinus*, northern flying squirrel, partial harvesting, red squirrel, *Tamias amoenus*, *Tamiasciurus hudsonicus*, yellow-pine chipmunk.

Forest managers are often faced with the challenge of maintaining diverse economic, social, and biological values in managed landscapes. Clear-cut harvesting creates an extended period when habitat for forest-dependent species is eliminated; hence, alternative harvesting systems such as partial cutting are increasingly used with the goal of mitigating the effects of timber harvesting on social and ecological values. Past research on the effects of partial harvesting has generally focused on tree regeneration and seedling survival in cutover areas (e.g., Childs and Flint 1987, DeLong and Butts 1994), the spread of forest pathogens such as armillaria (*Armillaria* sp.) or mountain pine beetle (*Dendroctonus ponderosae*; e.g., Amman et al. 1988, Davis and Machmer 1998), and more recently, on maintaining biological diversity and ecological function (e.g., Waters and Zabel 1995, Lehmkuhl et al. 1999, Zenner 2000, Sullivan et al. 2001).

Retaining live trees and other stand attributes can have a positive effect on species that depend directly on forest resources (e.g., conifer foliage, conifer seeds, and ectomycorrhizal fungi) to meet life-history requirements (e.g., Patton et al. 1985, Beese and Bryant 1999, Carey 2001, Lance and Phinney 2001). For example, species richness and community composition of birds in partially harvested stands can be similar to unharvested forests when residual trees and snags are maintained (Norton and Hannon 1997, Chambers et al. 1999, Schieck and Hobson 2000). However, partial-retention logging methods are diverse and their effectiveness at enhancing the short- and long-term persistence or recolonization of forest-dependent species, including sciurids, remains largely unknown (Lehmkuhl et al. 1999, Noss 1999).

In Douglas-fir (*Pseudotsuga menziesii glauca*) forests of central British Columbia, Canada, there are 3 common squirrel species each with unique life-history requirements: red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), and yellow-pine chipmunks (*Tamias amoenus*). Red squirrels are associated with coniferous forests and feed on seasonally abundant foods such as fungi, conifer buds, and rose hips (Smith 1968a, Rusch and Reeder 1978, Sullivan 1990). However, the staple of their diet is conifer seed and they defend individual territories necessary for exclusive access to this resource (Smith 1968a,b; Kemp and Keith 1970). Northern flying squirrels are common in mature and old-growth forests throughout much of North America (Wells-Gosling and Heaney 1984). They are nocturnal and forage extensively on the sporocarps of ectomycorrhizal fungi and epiphytic lichens throughout the year (Maser et al. 1978, Carey 1995, Currah et al. 2000). Northern flying squirrels have received considerable attention in the Pacific Northwest because they are the primary prey species for the Northern spotted owl (*Strix occidentalis*; Carey et al. 1992). Yellow-pine chipmunks inhabit early seral and open forests dominated by shrubs, forbs, and grasses (Chappell 1978, Sutton 1992). The close association between these squirrel species and a variety of stand-level forest attributes make them useful as indicator species in large-scale silvicultural trials. The red squirrel and northern flying squirrel are forest-dependent and their response to partial-cut harvesting should reflect the efficacy of these management systems for maintaining the habitat structures they require. However, the amount and pattern of residual structure that is needed to maintain these species is unknown. In contrast, a response by yellow-pine chipmunks will likely reflect

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7) logging from 1 year to 4 years postlogging ($M_{\text{harvesting}}$) independent of logging intensity or pattern, and 8) not affected by harvesting treatments (M_{null}).

For all other demographic variables we did not have sufficient data to conduct analyses by year. As a result, we analyzed survival using data combined across years by replicate (1–3 yr postlogging). For squirrel survival we hypothesized that the response of squirrels was affected by 1) intensity of logging from 1 year to 3 years postlogging ($M_{\text{intensity } 94-96}$), 2) pattern of logging from 1 year to 3 years postlogging ($M_{\text{pattern } 94-96}$), 3) logging from 1 year to 3 years postlogging ($M_{\text{harvesting}}$) independent of logging intensity or pattern, and 4) not affected by harvesting treatments (M_{null}).

Finally, we analyzed recruitment and body mass using overall averages for each replicate site from 1994 to 1997. As a result, our hypotheses for recruitment and body mass followed density models 1, 4, 7, and 8.

We developed all intensity of logging models using linear regression. For all parameters in these regression models (i.e., density, recruitment, survival, and body mass) the explanatory variable was intensity of logging (% residual basal area relative to controls).

We analyzed density using the repeated-measures linear mixed-effect model with fixed treatment and time effects, and we evaluated goodness-of-fit (McFadden's pseudo R^2) for $M_{\text{intensity } 95-97}$ using a chi-squared test. We treated grids as a random effect because of nonindependence between years. We analyzed recruitment, survival, and body mass using analysis of variance and regression models.

We selected models for squirrel density using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). We selected best-fit models for squirrel recruitment, survival, and body mass using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 1998). We calculated the ΔAIC_c values as the absolute difference between a given model and the most parsimonious model ($\Delta\text{AIC}_c = 0$). Using these values, we then calculated Akaike weights (w_i) as an index of relative plausibility. The ratio of w_i between any 2 models is the relative weight of support of any particular model over another (Burnham and Anderson 1998).

RESULTS

Average intensity of logging on all harvested silvicultural treatments was 42% (SE = 4.8, $n = 10$; Table 1). Across all logged treatments, average residual stem density of live trees >17 cm diameter at breast height was 199 trees/ha (SE = 16.3, $n = 10$).

In 29,800 trap-nights we captured 640 red squirrels 3,038 times, 245 northern flying squirrels 651 times, and 417 yellow-pine chipmunks 784 times. Overall, the proportion of individual animals captured on multiple experimental units in one year was 8.4% (54 animals) for red squirrels, 5.7% (14 animals) for northern flying squirrels, and 0.5% (2 animals) for yellow-pine chipmunks. Red squirrels, northern flying squirrels, and yellow-pine chipmunks were approx-

imately equally catchable, satisfying a critical assumption of Jolly-Seber estimation techniques.

Density

Red squirrel density did not vary with harvesting treatment in the first year after logging (Table 2). From 2 years to 4 years after logging, red squirrel density declined with intensity of tree removal (Table 2; Fig. 2a). Red squirrel density in control sites averaged 16.3 animals per 9 ha (SE = 1.8, $n = 2$) and declined to 9.3 animals per 9 ha (SE = 1.2, $n = 5$) after 4 years in all treatments with 50–63% tree removal. Logging had a negative effect on northern flying squirrel density within 1 year that continued to 4 years after logging, irrespective of intensity or pattern of removal (Table 2; Fig. 2b). Northern flying squirrel density in control sites was 5.8 animals per 9 ha (SE = 1.6, $n = 2$) and declined to 2.3 animals per 9 ha (SE = 0.3, $n = 10$) in logged treatments.

In the third and fourth year after logging (1996–1997), yellow-pine chipmunk density increased in response to intensity of tree removal (Table 2; Fig. 2c). Density in control sites averaged 0.67 animals per 9 ha (SE = 0.07, $n = 2$) and increased to 6.2 animals per 9 ha (SE = 1.8, $n = 5$) in treatments with 50–63% tree removal.

Goodness-of-fit was significant for red squirrels (pseudo $R^2 = 0.12$, $\chi^2 < 0.001$), northern flying squirrels (pseudo $R^2 = 0.12$, $\chi^2 < 0.001$), and yellow-pine chipmunk density (pseudo $R^2 = 0.10$, $\chi^2 < 0.001$). This indicates that a consistent pattern is being expressed in our data that can be explained by the intensity of tree removal from 2 years to 4 years postlogging.

Recruitment

We found little evidence that red squirrel or northern flying squirrel recruitment was affected by harvesting (Table 2). Yellow-pine chipmunk recruitment may have increased in harvested treatments (Table 2). Yellow-pine chipmunk recruitment averaged 25% (SE = 9.8, $n = 2$) in controls and increased to 35% (SE = 2.1, $n = 10$) in harvested treatments. Overall average recruitment from 1 year to 3 years after logging was 52% (SE = 1.9, $n = 12$) for red squirrels, 45% (SE = 3.0, $n = 12$) for northern flying squirrels, and 33% (SE = 2.4, $n = 12$) for yellow-pine chipmunks.

Survival

Red squirrel, northern flying squirrel, and yellow-pine chipmunk survival did not vary with harvesting treatment (Table 2). Monthly survival (May to Nov) averaged 0.93 (SE = 0.005, $n = 12$) for red squirrels, 0.91 (SE = 0.014, $n = 12$) for northern flying squirrels, and 0.90 (SE = 0.013, $n = 12$) for yellow-pine chipmunks. Average overwinter survival (Dec to Apr) was 0.92 (SE = 0.023, $n = 12$) for red squirrels, 0.92 (SE = 0.029, $n = 12$) for northern flying squirrels, and 0.83 (SE = 0.027, $n = 12$) for yellow-pine chipmunks.

Body Mass

Body mass of male red squirrels declined with increased logging intensity ($M_{\text{intensity } 94-97}$, $y = -0.1457x + 222.5$ g,

16.3
↓
9.3
=
43%
decline

Table 2. Akaike's Information Criterion (adjusted for small sample size; AIC_c)-model selection for squirrel density, recruitment, survival, male body mass and female body mass at the Opax Mountain silvicultural systems site near Kamloops, British Columbia, Canada, 1994–1997.

Red squirrel					Northern flying squirrel					Yellow-pine chipmunk				
Model	K^a	RSS or $-LnI^b$	ΔAIC_c^c	$AIC_c \text{ wt}^d$	Model	K	RSS or $-LnI$	ΔAIC_c	$AIC_c \text{ wt}^d$	Model	K	RSS or $-LnI$	ΔAIC_c^c	$AIC_c \text{ wt}^d$
Density														
$M_{\text{intensity 95-97}}$	15	-149.6	0.0	1.00	$M_{\text{harvesting}}$	13	-77.2	0.0	0.98	$M_{\text{intensity 96-97}}$	15	-107.9	0	1.00
Recruitment														
M_{null}	2	452.5	0.0	0.72	M_{null}	2	1,201.7	0.0	0.67	M_{null}	2	757.2	0.0	0.45
$M_{\text{intensity 94-97}}$	3	449.4	3.3	0.14	$M_{\text{intensity 94-97}}$	3	1,106.3	2.4	0.20	$M_{\text{harvesting}}$	3	599.4	0.6	0.34
$M_{\text{harvesting}}$	3	451.7	3.4	0.14	$M_{\text{harvesting}}$	3	1,196.6	3.3	0.13	$M_{\text{intensity 94-97}}$	3	645.5	1.5	0.22
Survival														
M_{null}	2	0.004	0.0	0.59	M_{null}	2	0.025	0	0.65	M_{null}	2	0.021	0	0.72
$M_{\text{harvesting}}$	3	0.003	1.8	0.24	$M_{\text{intensity 94-96}}$	3	0.023	2.3	0.21	$M_{\text{harvesting}}$	3	0.021	3.3	0.14
$M_{\text{intensity 94-96}}$	3	0.004	3.1	0.13	$M_{\text{harvesting}}$	3	0.025	3.0	0.14	$M_{\text{intensity 94-96}}$	3	0.021	3.4	0.13
M mass														
$M_{\text{intensity 94-97}}$	3	203.3	0.0	0.60	M_{null}	2	1,412.1	0.0	0.62	$M_{\text{pattern 94-97}}$	5	5.3	0.0	0.59
M_{null}	2	313.7	1.8	0.24	$M_{\text{harvesting}}$	3	1,294.3	2.3	0.19	$M_{\text{harvesting}}$	3	15.0	2.2	0.19
$M_{\text{harvesting}}$	3	252.7	2.6	0.16	$M_{\text{intensity 94-97}}$	3	1,330.4	2.7	0.16	$M_{\text{intensity 94-97}}$	3	15.2	2.5	0.17
F mass														
M_{null}	2	139.0	0.0	0.54	M_{null}	2	473.4	0.0	0.71	M_{null}	2	42.6	0.0	0.60
$M_{\text{harvesting}}$	3	115.1	1.1	0.31	$M_{\text{intensity 94-97}}$	3	457.0	3.0	0.16	$M_{\text{harvesting}}$	3	36.0	1.5	0.28
$M_{\text{intensity 94-97}}$	3	136.8	3.2	0.11	$M_{\text{harvesting}}$	3	473.3	3.4	0.13	$M_{\text{intensity 94-97}}$	3	42.5	3.4	0.11

^a No. of estimable parameters in each model.

^b Residual sums of sq. (RSS) or negative log likelihood ($-LnI$) for density models.

^c AIC_c , difference relative to the smallest AIC_c value for each model set. We used AIC_c for density model selection.

^d Models are sorted from highest to lowest $AIC_c \text{ wt}$. Only models with $>0.10 AIC_c \text{ wt}$ are shown. We used AIC_c for density model selection.

$R^2 = 0.35$; Table 2). Average body mass decreased from 222.5 g (SE = 2.06, $n = 2$) in controls to 215.0 g (SE = 2.47, $n = 5$) in treatments with 50–63% basal-area removal. Body mass of female red squirrels ($\bar{x} = 213.5$, SE = 1.03, $n = 12$) did not seem to vary with harvesting treatment (Table 2). Similarly, body mass of male ($\bar{x} = 137.5$ g, SE = 3.27, $n = 12$) and female ($\bar{x} = 141.7$ g, SE = 1.89, $n = 12$) northern flying squirrels varied little with harvesting treatment (Table 2). Differences in the pattern of logging best explained the body mass of male yellow-pine chipmunks (Table 2). Adult males averaged 48.8 g (SE = 1.25, $n = 2$) in the control, 50.3 g (SE = 0.21, $n = 4$) in the patch-cut treatments, 51.1 g (SE = 0.37, $n = 4$) in the uniform treatments, and 53.0 g (SE = 0.01, $n = 2$) in the reserve treatments. Average body mass of female yellow-pine chipmunks was 55.9 g (SE = 0.62, $n = 12$) and did not seem to be affected by the intensity or pattern of harvest treatments (Table 2).

DISCUSSION

In the dry Douglas-fir forests we studied, we observed different responses to partial-cut forest harvesting by 3 species of forest-dwelling sciurids. When approximately 50% of the timber volume was removed from the stand, northern flying squirrel abundance decreased by an average of 60%, red squirrel abundance diminished by approximately 40%, and yellow-pine chipmunk abundance increased 700%. These differences likely reflect the different response of each of these species to the partial removal of forest cover through harvesting.

Timber harvesting initiates complex structural changes in a stand related to the removal of mature stems, increased light penetration to the understory with associated micro-

climate and vegetation changes (Riegel and Miller 1992, Thomas et al. 1999, Thysell and Carey 2001), and the loss of snags through physical damage or the creation of a safe work area. The abundance of species such as red squirrels that are dependent on conifer seeds (Smith 1968a,b, Kemp and Keith 1970) should diminish as mature seed-producing trees are removed. In our study, red squirrels initially showed little response to forest harvesting, likely due to the presence of residual conifer seed in food caches that remained intact in the harvested areas. In most North American coniferous forests, red squirrels store conifer cones in a single hoard, which may offset food shortages for up to 2 consecutive winters (Smith 1968b, Rusch and Reeder 1978). We speculate that once the cached stores of conifer seed became depleted approximately 1 year after harvesting, red squirrel densities then adjusted to the postharvest habitat conditions as animals died or abandoned their territories.

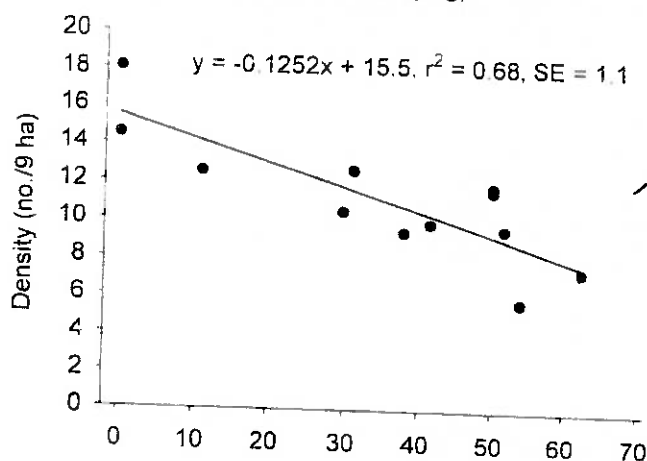
Several studies have examined the abundance of northern flying squirrels in partially harvested stands. In white (*Abies concolor*) and red (*A. magnifica*) fir shelterwood stands (5–7 yr postlogging), Waters and Zabel (1995) found that northern flying squirrel densities averaged 88% lower where the reduction in basal area was approximately 80%. In a study of 60–70-year-old coastal Douglas-fir forests, Carey (2000) noted varied results. Density of northern flying squirrels in stands that had an uneven-aged canopy, high levels of coarse woody debris (CWD), and 30% basal-area thinning was 41% lower 5–7 years after logging. In contrast, there was no change in northern flying squirrel density in stands with an even-aged canopy, low volumes of CWD, and a 24% basal-area thinning. Ransome (2001) found no effect of a 52%

tree removal on northern flying squirrel density or survival in the first 2 years after logging in 60-year-old coastal western hemlock (*Tsuga heterophylla*) stands. It is not clear why we observed an immediate and pronounced reduction in northern flying squirrel density in partially logged stands whereas Ransome (2001) found none. Ransome (2001) suggested that logging would have little effect on the density of northern flying squirrels when >350 dominant trees/ha were retained. We conducted our study in a dry inland forest type where the high-removal treatments had a much lower average retention of 199 trees per ha (>17 cm dbh). It is possible that changes to the within-stand microclimate were more severe in the dry forest system that we studied and hence has a greater effect on northern flying squirrel habitat quality.

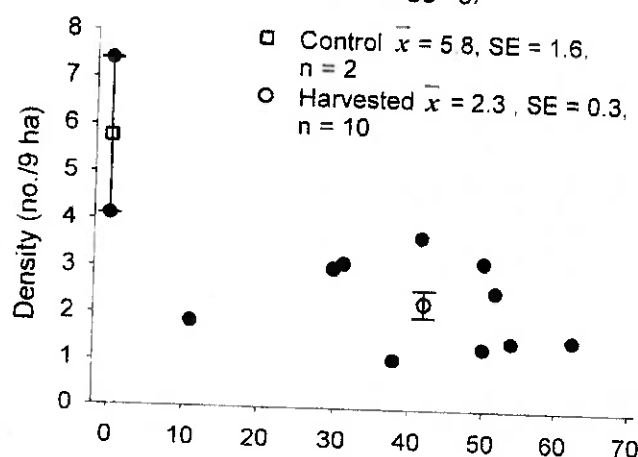
Although little research has been conducted on the response of tree squirrel density to food deletion, food supplementation studies support the hypothesis that abundance of red squirrels (Sullivan 1990, Klenner and Krebs 1991, Ransome and Sullivan 1997) and northern flying squirrels (Ransome and Sullivan 1997, 2004) are limited by food availability. In light of these experimental studies, we suggest that a reduction in food availability resulting from removal of seed-producing mature trees during harvesting is the primary reason that we observed a reduction in red squirrel abundance with increased logging intensity. At the scale of individual animals, red squirrel survival and recruitment did not seem to differ across the range of logging intensity examined in our study, suggesting that predation is an unlikely cause of the observed changes in density.

The majority of research on northern flying squirrels suggests that food availability often limits population density (Waters and Zabel 1995, North et al. 1997, Carey et al. 1999). Sporocarps of hypogeous fungi (truffles) are clearly important in the diet of northern flying squirrels (Maser et al. 1985, Currah et al. 2000, Pyare and Longland 2001). In the western United States, truffle abundance can be 5–8 times lower in young stands regenerating after clear-cut harvesting than in naturally regenerating mature and old-growth stands (Amaranthus et al. 1994, North et al. 1997). Low truffle biomass in managed young stands may limit northern flying squirrel density, particularly during the winter when truffles are least available (North et al. 1997, Colgan et al. 1999). Two studies, both from the western United States, have examined truffles in partially logged stands. Waters and Zabel (1995) found an 85% reduction in the occurrence of truffles in recently logged shelterwood stands. Similarly, Colgan et al. (1999), working in 70-year-old coastal Douglas-fir stands, found that variable-density thinning generally reduced truffle biomass by 50% when compared to unthinned stands. A single study from the much cooler climate of northeastern Alberta found that the sporocarps of epigeous fungi (mushrooms) replaced truffles as the most common food for northern flying squirrels during winter (Currah et al. 2000). Similar to truffles, the short-term abundance of mushrooms may decline following logging (Bradbury et al. 1998). Although it is not clear if

(a) Red squirrels (2–4 yr postlogging)



(b) Flying squirrels (1–4 yr postlogging)



(c) Yellow-pine chipmunk (3–4 yr postlogging)

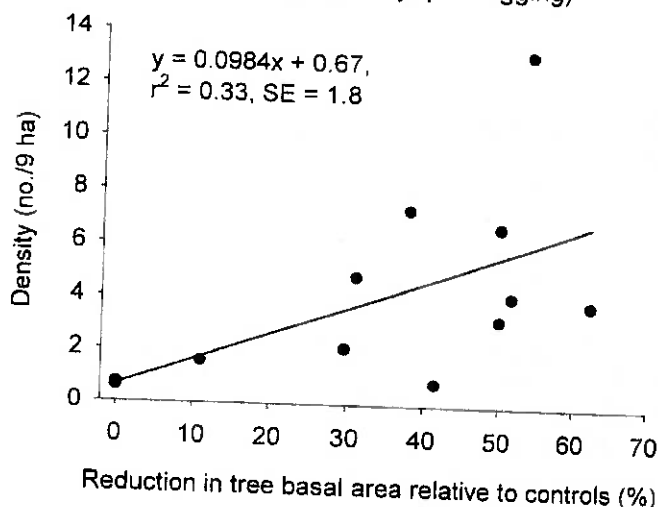


Figure 2. Density of (a) red squirrels, (b) northern flying squirrels, and (c) yellow-pine chipmunks at the Opax Mountain silvicultural systems site near Kamloops, British Columbia, Canada, 1994–1997.

truffles or mushrooms were most important to northern flying squirrels in our study, it seems likely that the abundance of fungal sporocarps, and thus, of northern flying squirrels, decreased in harvested stands.

Unlike red squirrels and northern flying squirrels, abundances of yellow-pine chipmunks increased in proportion to the stand volume removed. The 2-year lag followed by a strong increase in the abundance of yellow-pine chipmunks is consistent with the lag in understory vegetation response we observed. In 1994, the first growing season after harvest at our study site, we noted little increase in understory vigor whereas, by 1996, grasses and forbs in logged treatments were well-established and often >1 m high. Sullivan and Sullivan (2001), also working in inland Douglas-fir forests, found that yellow-pine chipmunk density was similar between heavily logged stands (basal area <2.5 m²/ha) and mature forests 1 year after harvesting, but abundance showed a strong increase in logged stands from 2 years to 4 years. Similarly, yellow-pine chipmunks were more abundant in low-density than in high-density young lodgepole pine stands (Sullivan and Klenner 2000, Sullivan et al. 2001). Early seral forest conditions provide abundant food resources for yellow-pine chipmunks, which are considered diet generalists, feeding on conifer seed (*Pinus* sp. and Douglas-fir), grass seed, fruiting bodies from shrubs (e.g., *Rosa* sp.) and herbs (e.g., *Clintonia uniflora*, *Fragaria virginiana*), and fungi (Chappell 1978, Maser et al. 1978, Sutton 1992). Although there is good evidence to suggest that chipmunk abundance is limited by food availability (Sullivan et al. 1983, 2001; Sullivan and Klenner 2000), chipmunks in early seral forests may also experience less competitive interference from red squirrels. Sullivan and Klenner (2000) suggested that yellow-pine chipmunks benefit from low red squirrel densities. In our study, yellow-pine chipmunks were often chased from food caches established by resident red squirrels (J. Herbers, Alberta Biodiversity Monitoring Institute, personal observation).

The changes in abundance we observed, with one species increasing and 2 others declining at different rates, is consistent with observations on the response of other vertebrate communities to partial cut or variable retention harvesting. Sullivan and Sullivan (2001) studied microtine rodents in relation to stand-level retention and noted that whereas *Microtus* sp. abundance increased with declining tree retention, red-backed vole (*Clethrionomys gapperi*) abundance decreased with declining tree retention. In a more diverse forest bird community, Norton and Hannon (1997), Lance and Phinney (2001), and Tittler et al. (2001) reported a similar pattern; early seral bird species increased in abundance in low-retention cut-blocks, whereas other species required within-block tree retention approaching ≥50% to maintain high abundances. These patterns of vertebrate abundance in relation to partial or clear-cut harvesting clearly indicates the need for diverse approaches to forest harvesting if all species are to be maintained across landscapes (Hansen et al. 1993). Our study on the response of forest sciurids to partial harvesting supports this

perspective and suggests forest sciurids may be a suitable group to monitor changes in the overall forest vertebrate community in relation to management practices.

Though statistically significant, we found that goodness-of-fit values for density models were low, suggesting that considerable sources of variance remained unaccounted for by our study design. This is likely a result of the low sample size limiting our ability to support statistical models that enabled interaction between logging intensity and logging pattern.

Our results apply only to mature managed stands where >35% (i.e., >10 m²/ha) of the basal area is retained. At lower retention levels, excessive dilution of habitat for small mammals that depend on mature forest attributes (Huggard 1994 in Ehrlich 1996; Ganzhorn et al. 1997) may strongly diminish habitat quality for some species.

MANAGEMENT IMPLICATIONS

The different responses by the 3 sciurids we monitored to the range of partial-cut harvesting treatments demonstrated that there was no single best harvesting treatment that was suitable for all 3 species. Up to 4 years postlogging, forest managers should anticipate an approximate 1:1 relationship between logging intensity and declining red squirrel density whereas maintaining a high abundance of flying squirrels in logged stands is unlikely regardless of logging pattern or intensity. Different harvesting systems need to be applied in a coordinated manner to maintain sciurid diversity in managed landscapes.

ACKNOWLEDGMENTS

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PROCEEDINGS OF A SYMPOSIUM ON

VULNERABILITY



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Hosted by the Montana Chapter of The Wildlife Society

**Montana State University
Bozeman, Montana
April 10 - 12, 1991**

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DEFINING ELK SECURITY: THE HILLIS PARADIGM

ABSTRACT

Elk vulnerability may be reduced, and hunter opportunity may be increased, by providing security areas for elk during the hunting season. We define security area requirements for land managers so that timber harvest decisions can reflect elk security needs.

To provide a reasonable level of bull survival, each security area must be a nonlinear block of hiding cover ≥ 250 acres in size and $\geq$ one-half mile from any open road. Collectively, these blocks must equal at least 30% of the analysis unit. Vegetation density, topography, road access, hunter-use patterns and elk movements are variables that must be considered when applying these guidelines. Examples are provided that illustrate how the security guidelines are applied in the field.

INTRODUCTION

Timber harvest affects elk vulnerability by changing the structure, size, juxtaposition and accessibility of security areas. Biologists have recently provided working definitions of "security," "security area," and "elk vulnerability" (Lyon and Christensen 1990). However, elk and timber managers still await research answers to current questions such as: "How large must a cover block be to provide effective security, how far must a security area be from a road, and how much of the area should provide security to meet elk vulnerability objectives?"

We developed guidelines for retaining elk security areas west of the Continental Divide in Montana. We suggest that the concepts presented here could assist managers in providing security areas elsewhere. We also hope this stimulates constructive criticism and research that improve the guidelines.

Special thanks go to S. D. Rose for helpful editorial comments. J. E. Firebaugh and R. E. Henderson provided technical reviews of the manuscript. We thank O. L. Daniels and C. W. Spoon for supporting development and application of these guidelines.

STUDY AREA

We devised guidelines applicable to the situations we know in the Clark Fork River drainage (excluding the Flathead River drainage). The area is characterized by steep slopes extensively forested by ponderosa pine, Douglas-fir, lodgepole pine, western larch and subalpine fir. Average elk populations and hunter numbers are at 30-year highs in the area, while the average bull/cow ratio observed by Montana Department of Fish, Wildlife and Parks (MDFWP) biologists in early spring has declined during the same period (MDFWP, Missoula, unpubl.

data). The majority of elk habitat in the area is managed by the Lolo, Bitterroot and Deerlodge National Forests; although substantial portions are owned by Plum Creek Timber Company, Champion International Corporation, other private landowners, Montana Department of State Lands and USDI Bureau of Land Management.

MANAGEMENT OBJECTIVES

Lonner and Cada (1982) proposed that, "hunting recreational opportunities are good when hunting season lengths are relatively long, harvest rates are uniform, and rules and regulations few. The present 35-day general elk-hunting season in Montana permits a diversity of choice [for hunters] with regard to time, weather conditions, hunter density and area. A lengthy hunting season has little meaning if the majority of the harvest occurs in the first few days."

Nine years since Lonner and Cada's (1982) contribution, MDFWP and the three national forests within the study area formally share the following objectives: 1) maintain the current, relatively unregulated, 5-week hunting season; 2) distribute the bull harvest evenly over the entire hunting season; and 3) maintain a desired level of mature bulls in the post-hunting season population (For. Plan, Lolo Natl. For., 1986; For. Plan, Bitterroot Natl. For., 1987; For. Plan, Deerlodge Natl. For., 1987; Draft Elk Manage. Plan, MDFWP, Helena, 1991). We developed guidelines to meet these objectives.

The agencies have decided to maintain habitat security levels that allow desired numbers of bull elk to escape harvest, rather than impose more restrictions on hunters (e.g., shorter hunting seasons, antler-point restrictions, limited licenses). The recreational opportunities resulting from this type of management are becoming increasingly rare nationwide (Anon. 1988).

DOCUMENTATION

We developed guidelines from the following background of knowledge:

1. Elk behavior changes in response to the hunting season (Marcum 1975; Morgantini and Hudson 1979, 1985; Canfield 1988; Lyon and Canfield 1991).

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2. Elk avoid areas adjacent to roads with vehicular traffic, especially during the hunting season (Marcum 1975, Perry and Overly 1976, Lyon 1979, Irwin and Peek 1983, Lyon 1983, Lyon et al. 1985, Lyon and Canfield 1991).

3. Elk spend more time in dense cover during hunting season than they do before the hunting season (Marcum 1975, Irwin and Peek 1983, Canfield 1988). Large cover-blocks contribute to security more than small blocks (Canfield 1988, Lyon and Canfield 1991).

4. Elk movements generally are confined to habitats within a traditionally used home range (Edge et al. 1985, Lyon et al. 1985, Edge et al. 1986).

5. Road closures may either increase or decrease elk vulnerability depending upon the influences of cover, topography and hunting pressure, both within and adjacent to a security area (Basile and Lonner 1979, Lyon et al. 1985).

SECURITY-AREA GUIDELINES

How Large Must a Cover Block Be?

Larger is better—To meet the hunting opportunity objectives outlined here, managers should strive to retain, perpetuate, or replace the largest security areas possible. We assume that as security areas increase in size, elk become harder for hunters to find, and liberal hunting opportunities become less costly in terms of elk vulnerability.

Minimum size—In the lower Clark Fork drainage, conditions are favorable for elk to elude hunters: cover is dense, terrain is steep, and forest communities are largely unfragmented. Lyon and Canfield (1991) found that elk in this area selected for large, connected, vegetation communities (i.e., forest blocks of similar canopy structure). All other factors held constant, 236-acre unfragmented communities met minimum security requirements for 60% of the radioed elk. For the purposes of these guidelines, 250 acres appears to be the minimum-sized area for providing security under favorable conditions; under less favorable conditions, the minimum must be >250 acres.

Variables to consider—Effective security areas may consist of several different cover-types if the block is relatively unfragmented. For example, regenerated cutting units that provide reasonable cover might be found within an effective security area (Canfield et al. 1986). Among security areas of the same size, one with the least amount of edge and the greatest width generally will be the most effective. Rugged topography may increase security if it substantially decreases the accessibility of the area to hunters. Wallows, springs and saddles may require more cover than other habitats because both hunters and elk recognize and target these destinations.

How Far Must a Security Area Be from a Road?

Minimum distance—Generally, security areas become more effective the farther they are from an open road. Considering documented road-avoidance by elk

(Lyon 1983, Lyon et al. 1985), the minimum distance between a security area and an open road should be one half mile. The function of this $\geq$ one half mile "buffer" is to reduce and disperse hunting pressure and harvest that is concentrated along open roads (Daneke 1980). Failure to accomplish this function will reduce the effective size of the security area and may render it ineffective.

Road design considerations

—Road-design features may inadvertently turn designated security areas into hunter destinations. For example, trailheads, turnouts and/or parking areas in close proximity to security areas will concentrate hunting pressure in the vicinity and increase elk vulnerability. Similarly, open roads located both above and below a security area on a slope will encourage hunters to walk through the security area.

Cover and terrain—When cover is poor and terrain is gentle, it may require a distance >one half mile from open roads before security is effective. In such situations, hunters may identify the security area from the road, and the gentle terrain will deter few hunters from hiking. Conversely, if the security area is hidden or difficult to reach from a road, elk may find security in situations < one half mile from an open road.

Closed roads—Roads may be closed (to motorized travel) to provide security and a buffer between security areas and open roads. However, the minimum distance between open roads and security areas increases as closed-road densities increase within both the security area and buffer. Closed roads located within security areas may increase elk vulnerability by providing hunters with walking and shooting lanes. Use of horses and increasing use of mountain bikes by hunters on closed roads allows them better access and increases elk vulnerability, compared to unroaded habitats. Therefore, roads within security areas should be kept to an absolute minimum.

How Much of the Area Should Provide Security?

Analysis unit—First, a standardized "habitat analysis unit" (Lyon and Christensen 1990) must be described. To be biologically meaningful, analysis unit boundaries should be defined by the elk herd home-range (Edge et al. 1986), and more specifically by the local herd home-range during hunting season. Typically, the hunting season home-range includes the local herd transitional-range and at least the upper edge of winter range. These boundaries should be verified in advance by radio telemetry, particularly where elk vulnerability is at issue. Without telemetry data, biologists should test their home-range predictions against the experience of reliable local hunters and outfitters. Analysis units should not be adjusted for land ownership; instead, they should reflect the cumulative habitat conditions perceived by elk.

Minimum amount of security—Our collective experience suggests elk vulnerability increases when less

than 30% of an analysis unit is comprised of security areas (Canfield 1991). Where bull survival objectives are high, it may be necessary to retain greater than 30% of the analysis unit in security.

Spatial arrangement—In conjunction with considering “how much security,” it is critical to consider spatial arrangement of security areas across the landscape. The arrangement should provide for the habitat needs of elk through the 5-week hunting season (e.g., forage and water). Providing security only on dry, harsh, steep slopes may allow elk to avoid hunters early in hunting season; however, it is unlikely that elk will stay in harsh sites for extended periods (Marcum 1975). Further, security areas should cover a wide elevational range so they are available to elk under various weather conditions (e.g., security areas at high elevations may be unusable by elk during periods of deep snow).

A few large, or several minimum-sized, security areas may comprise the same combined proportion of an analysis unit. The best balance between security-area sizes and numbers for an analysis unit will result from creative thinking firmly based on knowledge of local elk-movement and hunting patterns.

APPLICATION OF THE MANAGEMENT GUIDELINES

We suggest that security areas should be ≥ 250 acres in size, $\geq$ one half mile from an open road, and should comprise $\geq 30\%$ of a valid analysis unit. Unquestioning adherence to these guidelines may lead to serious misapplications and should be avoided. We believe the guidelines are properly applied when used to compare relative security levels in an analysis unit over time or to compare and evaluate the cumulative impacts of various timber-harvest alternatives on security. These guidelines represent minimums and do not necessarily justify reducing security to meet these levels (i.e., if 50% of an analysis unit is security, do not assume that 20% of the unit is excess security).

Inferences from detailed knowledge of a local elk herd—such as that typically obtained by radio telemetry—should override these management guidelines whenever discrepancies occur. For example, radioed elk have shown us site-specific exceptions where security is provided along highways or in small cover-blocks that hunters do not find. Similarly, traditional migration corridors and other elk concentration areas, if known, may deserve special considerations that are not covered by these guidelines (USDA 1991).

A comprehensive, sustained timber-management planning effort is required to obtain the greatest benefits from these guidelines. Radio-telemetry data should be collected ≥ 1 before year preparing alternative management strategies, and it may take ≥ 1 year to budget and prepare for a projected telemetry effort. Future timber harvest rotations, and recruitment of new security areas, should be projected to evaluate the best options for any proposed timber sale. Proposed timber harvests in remote and heavily forested analysis units should be carefully

approached because the rare opportunity exists to retain elk security by design in these units, rather than by default as dictated by past logging practices.

In analyzing security requirements for a specific area, interpretation of the guidelines is needed to ensure that the result makes biological sense for local conditions. The point of designating elk security areas is not to meet some generalized guidelines, but to provide functional habitat.

We present examples of actual management problems we have addressed, to illustrate: 1) guideline adjustments that made designated security areas reflect reality, and (2) provisions for meeting present and future security needs.

Example 1

The Sequoia-Brewster area lies about 20 miles from Missoula. The area's entrance road ends at a gate on level terrain (Fig. 1). The ease of walking in the area and the concentration of hunters at the end of the road suggested to us that an area only one half mile from the parking area would not provide adequate security. Therefore, the buffer between the parking and security areas was increased to 1 mile.

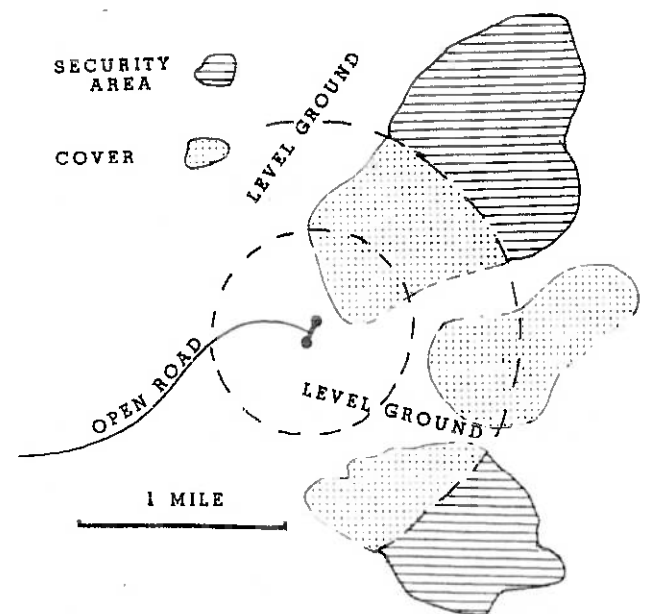


Figure 1. Sequoia-Brewster area, showing the relationship of security to an open road, recognizing the trailhead, level ground, and concentrated use. The one half mile zone was increased to 1 mile.

Example 2

The Tujo area includes a ridge between two parallel, creek-bottom roads; the two roads are connected by a road that switchbacks over the steep ridge (Fig. 2). This connecting road affects security in two ways: 1) its zigzag path accesses a large area and reduces the size of security areas A, B, and C (Fig. 2); and 2) it provides easy access to the ridgetop. Hunters can drive to the top and walk on a level, closed road into security area A. Likely hunting routes from the ridgetop to the creekside roads (and often to a second vehicle) are all downhill.

Keeping the connecting road open during the hunting season seriously compromises the protection we would expect from a large (2,400-acre) block such as security area A. To increase the area and quality of security, we proposed closing the connecting road during the hunting season. Since much of the area's popularity is due to the easy access provided by the open connecting road, public involvement on the issue is planned.

Example 3

The Sapphire Divide area (23,000 acres) lies 25 miles southeast of Missoula. The area is unusual because past logging was concentrated in the high-elevation basins along a major ridgetop-road. This fragmented the productive habitats that would have made good security areas. The 13% of the area that now provides security is all located in low- to mid-elevation sites that are low in productivity and characterized by steep, rocky ground.

Radio-tracking studies (Marcum 1975) in the 1970s showed that Sapphire Divide elk used the heavily logged, high elevations until hunting season. When hunters entered the area along the ridgetop road, elk immediately dropped down to the steep, dry slopes below. The elk adopted a weekly pattern of movement, returning to the productive, higher areas at mid-week and fleeing to the unproductive secure areas on weekends (when hunting pressure was highest). Thus the security areas were not only inadequate in acreage, they also were located in the

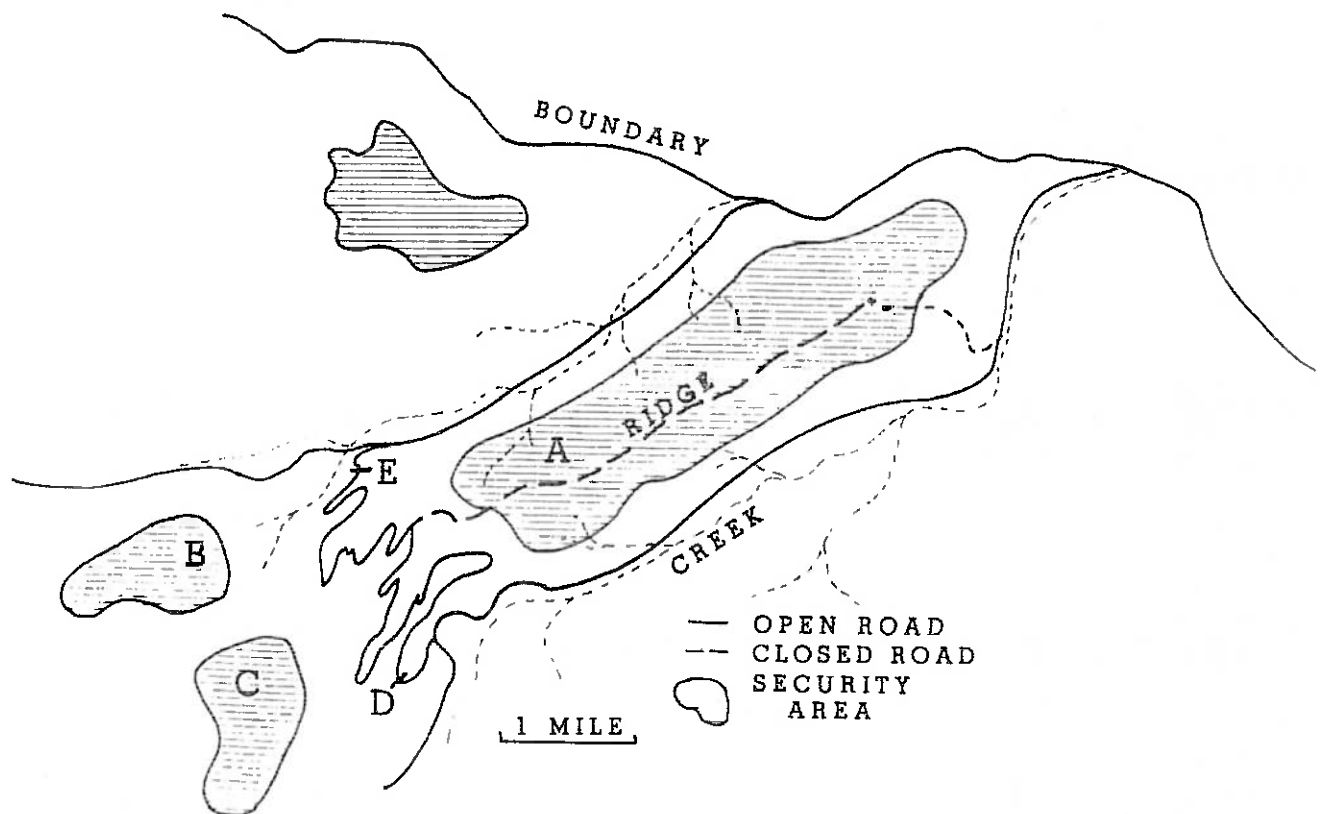


Figure 2. Tujo area, showing how security area A is affected by the ridgetop closed road. The proposed solution is to close the connecting road at points D and E.

wrong place. This made bulls especially vulnerable.

Predictably, the bull/cow ratio of this elk population is extremely low. After the 1989 hunting season, this ratio had declined to 3:100 (J.E. Firebaugh, MDFWP, Missoula, pers. commun.), suggesting that bull mortality due to hunting is very high.

To recover security in this analysis area, we first proposed to decrease hunter access to the high-elevation basins by closing entry roads near the points where they cross the divide from the west (Fig. 3). Second, to allow recovery of large cover-blocks in the productive, high-elevation basins, we developed a long-term strategy for the

spatial arrangement of timber harvest: deferring timber harvest in designated large blocks (Fig. 3) to allow contiguous areas to regain cover at the same time, and reduce the area's fragmentation. Third, future timber harvests will be designed to minimize fragmentation by concentrating logging in small areas not currently providing security. The initial logging entries will revisit previously logged land, joining (in effect) the scattered, recovering units (Fig. 4). This will create a block of recovered cutting-units that will provide the next generation of security, totalling about 25% of the analysis unit by the year 2000.

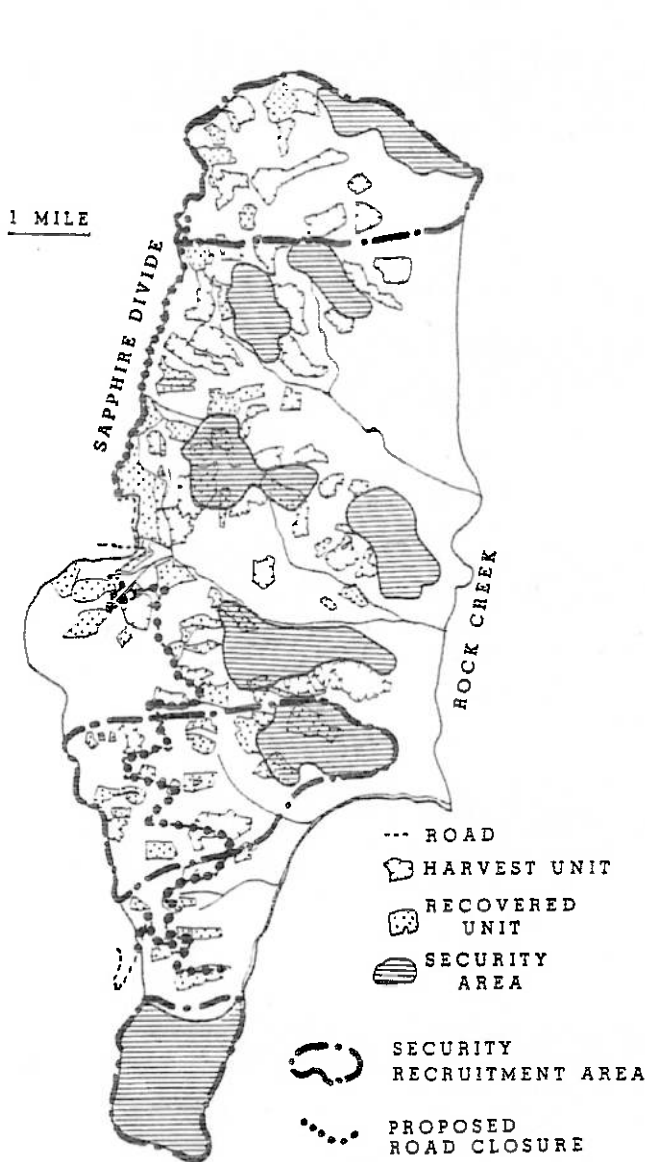


Figure 3. *Sapphire Divide area, showing designated security recruitment areas and roads proposed for closure. Note how the past harvest pattern has fragmented cover.*

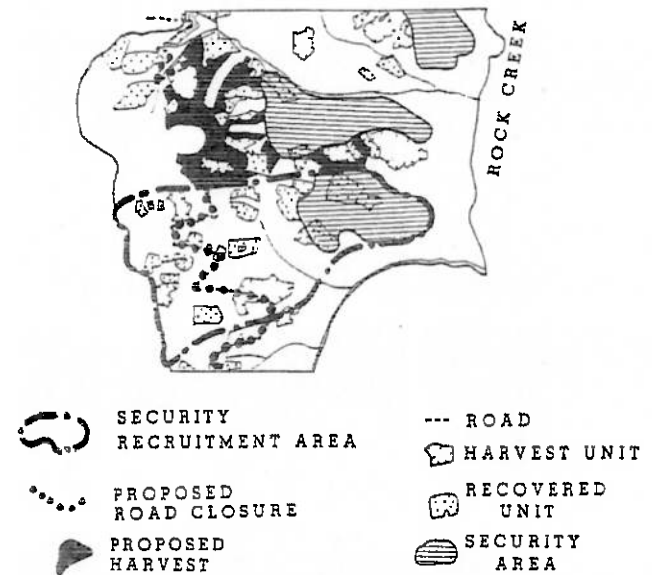


Figure 4. *South Sapphire Divide area, showing a clustered timber harvest strategy designed to create a large block of future security. Note how proposed cutting units are adjacent to recovered harvest units.*

CONCLUSIONS

During the last year, these guidelines were applied to nine elk herd-units involving 14 timber sales. Two disturbing trends were discovered. First, most herd units already had less than the minimum 30% security due to past timber harvest; in many of these cases, there were strong indications that bull survival was declining or at risk. Second, even in situations where security was substantially less than 30%, all remaining security stands were targeted for timber harvest. This indicates that timber harvest decisions made over the next few years will potentially severely impact remaining security and, ultimately, hunter opportunity.

Additional research is needed to test and refine these guidelines. However, based on the rapid, apparent decline of security, it is critical that we begin applying these guidelines immediately. Planning must not only address the quality and spatial arrangement of existing security areas, but also must provide for the regeneration of replacement security areas where a sustained timber harvest is desired.

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Understanding and predicting habitat for wildlife conservation: the case of Canada lynx at the range periphery

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Abstract. Ecologists and managers are motivated to predict the distribution of animals across landscapes as well as understand the mechanisms giving rise to that distribution. Satisfying this motivation requires an integrated framework that characterizes multi-scale habitat use and selection, as well as builds predictive models such as resource selection functions. However, the assumption of constant habitat use or selection is often made in such analyses, which ignores the possibility that individuals experiencing different conditions might respond differently. Assessing functional responses in habitat use evaluates how animal behavior changes with differing environmental conditions, which has basic and applied utility. Here, we combined these ideas into an integrated process that characterizes habitat relationships, predicts habitat, and assesses behavioral differences with changing environmental conditions. Our species of interest was Canada lynx (*Lynx canadensis*) in the Northern Rocky Mountains, which is a rare and federally threatened forest carnivore. Through our process, we developed multi-scale predictions of lynx distribution and learned that across scales and seasons, lynx use more mature, spruce-fir forests than any other structure stage or species. Intermediate snow depths and the distribution of snowshoe hares (*Lepus americanus*) were the strongest predictors of where lynx selected their home ranges. Within their home ranges, female and male lynx increasingly used advanced regeneration forest structures as they became more available (up to a maximum availability of 40%). These patterns supported the bottom-up mechanisms regulating Canada lynx in that advanced regeneration generally provides the most abundant snowshoe hares, while mature forest is where lynx appear to hunt efficiently. However, lynx exhibited decreasing use of stand initiation structures (up to a maximum availability of 25%). Land managers have an opportunity to promote lynx habitat in the form of advanced regeneration, but are required to go through the stand initiation phase. Thus, managers can apply the relative proportions of forest structure classes along with our response curves to inform landscape actions (e.g., timber harvest) targeted at facilitating the forest mosaic used and selected by Canada lynx. Collectively, the insights gleaned from our approach advance habitat conservation efforts and consequently are of broad utility to applied ecologists and managers.

Key words: functional response; habitat selection; habitat use; *Lynx canadensis*; resource selection function; scale-integrated selection function.

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AR= 55 km²
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that were equal in area to the median lynx home range (55 km²).

At the third order of selection, we used only our GPS data that we separated into two seasons, winter (November–March) and summer (April–October). For each season, we constructed individual home ranges (i.e., 95% MCP), which resulted in 64 and 60 individuals sampled in winter and summer, respectively. We used individual locations within 95% MCPs (winter = 60,036 locations, summer = 96,291 locations) to sample resource use by Canada lynx (winter: median = 722 locations/individual, range = 113–2972; summer: median = 1433 locations/individual, range = 61–4474). We sampled availability for each individual by randomly allocating

locations (ratio = 1:1 for used and available locations) in both winter and summer home ranges. To build our home ranges for Canada lynx, we used the adehabitatHR package (Calenge 2006) in program R (R Core Team 2016) and we used standard tools in ArcGIS (ESRI 2011) to build our samples of availability.

Resource variables

We characterized our study area using a targeted suite of biotic and abiotic covariates that we expected to influence resource use and selection by Canada lynx (Table 1). We characterized abiotic characteristics using topographic metrics including (1) topographic roughness (Jenness 2004), (2) heat load index (McCune and Keon

Table 1. Resource variables used in analyses of habitat use, habitat selection, and functional responses for Canada lynx (*Lynx canadensis*) in western Montana, USA.

Variable	Units	Base resolution (m ²)	Order	Resolution (m ²)	Reference
Cover					
PICO canopy cover	%	30	Both	100, 500	Savage et al. (2015)
PIEN-ABLA canopy cover	%	30	Both	250, 250	Savage et al. (2015)
LAOC canopy cover	%	30	Both	250, 250	Savage et al. (2015)
PSME canopy cover	%	30	Both	100, 100	Savage et al. (2015)
Horizontal cover	%	30	Both	250, 250	Holbrook et al. (2017)
Forest structure					
Proportion of sparse forest	Proportion	30	Both	250, 250	Savage and Lawrence (2017)
Proportion of stand initiation forest	Proportion	30	Both	250, 500	Savage and Lawrence (2017)
Proportion of advanced regenerating forest	Proportion	30	Both	500, 250	Savage and Lawrence (2017)
Proportion of mature forest	Proportion	30	Both	100, 100	Savage and Lawrence (2017)
Climate					
Mean snow depth on 1 April 2005–2013†	m	1000	2	—	NOHRSC (2004)
Topography					
Roughness	Index	30	Both	500, 500	Jenness (2004)
Heat load index	Index	30	3	250, 250	McCune and Keon (2002)
Topographic position index	Index	30	3	500, 250	Guisan et al. (1999)
Prey					
Snowshoe hare occupancy‡	Probability	Multi-scale	Both	NA, NA	Holbrook et al. (2017)
Snowshoe hare intensity of use‡	Pellets/Krebs plot	Multi-scale	Both	NA, NA	Holbrook et al. (2017)

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes; RSF, resource selection function. Covariate codes PICO, PIEN-ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively. "Order" indicates whether the covariate was used for RSFs at the second order (2), third order (3), or both (both). "Resolution" indicates the scale for a particular covariate that was selected based on lowest AIC_c during winter (W) and summer (S), respectively, which was subsequently used in RSFs at the third order.

† Mean snow depth was not included in our third-order RSF models because the resolution (1000 m²) was too coarse.

‡ Snowshoe hare occupancy or intensity of use across multiple scales was not assessed because they were multi-scale composites (Holbrook et al. 2017).

Table 2. Descriptions of forest structure classes using metrics from the USDA Forest Service Forest Inventory and Analysis program within modeled structure classes in Canada lynx (*Lynx canadensis*) habitat as defined by our RSF (i.e., score of 6–10 from our winter scale-integrated model) in western Montana, USA.

Structural class	General description
Sparse	Mixed-conifer stands (Appendix S1) that are sparsely stocked (naturally) or mechanically thinned, which tend to be younger (i.e., ~10–20 yr old) but can occur at any age. Sparse stands exhibited a median basal area-weighted dbh of 6 inches or 16 cm (IQR = 0–11 inches or 0–27 cm), 28% canopy cover (IQR = 8–49%), and a median estimated tree height of 34 ft or 10 m (IQR = 1–52 ft or 0.31–16 m). Median basal area of sparse stands was 40 ft ² /acre or 9 m ² /ha (IQR = 1–101 ft ² /acre or 0.23–23 m ² /ha), while tree density for trees larger than 5 inches (12.7 cm) was 48 trees/acre or 119 trees/ha (IQR = 0–144 trees/acre or 0–357 trees/ha). Tree density for trees <5 inches (12.7 cm) was 900 trees/acre or 2223 trees/ha (IQR = 0–3000 trees/acre or 0–7410 trees/ha).
Stand initiation	Stands that have few trees and an open canopy, and are a result of recent (e.g., ≤5 yr) disturbance (forest harvest or severe fire). Stand initiation exhibited a median basal area-weighted dbh of 0 inches and cm (IQR = 0–8 inches or 0–20 cm), 8% canopy cover (IQR = 0–36%), and a median estimated tree height of 1 foot or 0.31 m (IQR = 0–50 ft or 0–16 m). Median basal area of stand initiation was 0 ft ² /acre or 0 m ² /ha (IQR = 0–55 ft ² /acre or 0–13 m ² /ha), while tree density for trees larger than 5 inches (12.7 cm) was 0 trees/acre and trees/ha (IQR = 0–75 trees/acre or 0–186 trees/ha). Tree density for trees <5 inches (12.7 cm) was 0 trees/acre and trees/ha (IQR = 0–2249 trees/acre or 0–5557 trees/ha).
Advanced regeneration	Early–mid-seral stands of age ~25–40 yr with a mixed species composition, but spruce-fir tends to occur the most frequently (Appendix S1). Advanced regeneration exhibited a median basal area-weighted dbh of 8 inches or 20 cm (IQR = 5–10 inches or 14–27 cm); however, of the 51 plots examined 70% of them were classified at size classes between 5 and 15 inches (12.7–38 cm). Advanced regeneration exhibited median canopy cover of 45% (IQR = 30–70%), median tree height of 51 ft or 16 m (IQR = 34–64 ft or 10–20 m), and median basal area of 89 ft ² /acre or 20 m ² /ha (IQR = 39–124 ft ² /acre or 9–28 m ² /ha). Tree density for trees larger than 5 inches (12.7 cm) was 167 trees/acre or 416 trees/ha (IQR = 72–289 trees/acre or 178–714 trees/ha). Tree density for trees <5 inches (12.7 cm) was 900 trees/acre or 2223 trees/ha (IQR = 150–2549 trees/acre or 370–6298 trees/ha).
Mature	Mid-seral stands of age ≥40 yr arranged in a multi-storied structure with a mixed species composition, but spruce-fir tends to occur twice as much as any other species (Appendix S1). Mature exhibited a median basal area-weighted dbh of 10 inches or 25 cm (IQR = 7–14 inches or 18–35 cm). However, of the 194 plots examined 45% were classified at size classes between 5 and 10 inches (12.7–25.4 cm), 25% at size classes between 10 and 15 inches (25.4–38 cm), and 21% of them were classified at size classes between 15 and 25 inches (38–64 cm). Mature exhibited median canopy cover of 56% (IQR = 40–70%), median tree height of 65 ft or 20 m (IQR = 53–88 ft or 16–27 m), and median basal area of 140 ft ² /acre or 32 m ² /ha (IQR = 91–209 ft ² /acre or 21–48 m ² /ha). Tree density for trees larger than 5 inches (12.7 cm) was 217 trees/acre or 535 trees/ha (IQR = 144–331 trees/acre or 357–818 trees/ha). Tree density for trees <5 inches (12.7 cm) was 1500 trees/acre or 3705 trees/ha (IQR = 300–4200 trees/acre or 741–10,374 trees/ha).

Notes: RSF, resource selection function. Forest inventory data were collected during 2005–2012, and the total sample size was 366 subplots (subplots = ~170 m²), which included 194, 51, 34, and 87 classified as mature, advanced regeneration, stand initiation, and sparse, respectively. English and metric units are presented. Abbreviations IQR and dbh indicate the interquartile range and diameter at breast height, respectively. The calculation for basal area-weighted dbh was as follows: $\Sigma(\text{tree basal area} \times \text{dbh})/\text{total basal area}$.

previous analyses of habitat selection and fitness–habitat relationships (Squires et al. 2008, 2010, McCann and Moen 2011, Simons-Legaard et al. 2013, Kosterman 2014), we expected a positive association between Canada lynx and structural classes exhibiting dense trees and closed canopies (e.g., mature and advanced regeneration). In contrast, we expected a negative effect of the open classes (e.g., sparse and stand initiation) on lynx habitat use and selection. Given the strong association between lynx and forest structure, we expected to observe behavioral shifts in habitat use by lynx with changing availabilities of forest structure (i.e., functional responses).

Finally, we developed maps of predicted snowshoe hare occupancy (classification error = 25%)

and intensity of use (root-mean-square error = 4.22) across the distribution of lynx in the Northern Rockies (Holbrook et al. 2017). These maps characterized a composite for dense forests with high horizontal cover that occurred in intermediate snow depths (see Holbrook et al. 2017 for additional details). We used these data within our analytical process to characterize potential prey resources for Canada lynx. We expected a positive effect of these metrics on lynx habitat use and predicted that snowshoe hare occupancy would likely be a parsimonious predictor for mapping habitat of Canada lynx. In addition, we expected to observe a functional response in habitat use for both snowshoe hare occupancy and intensity of use (i.e., more disproportionate use at low values

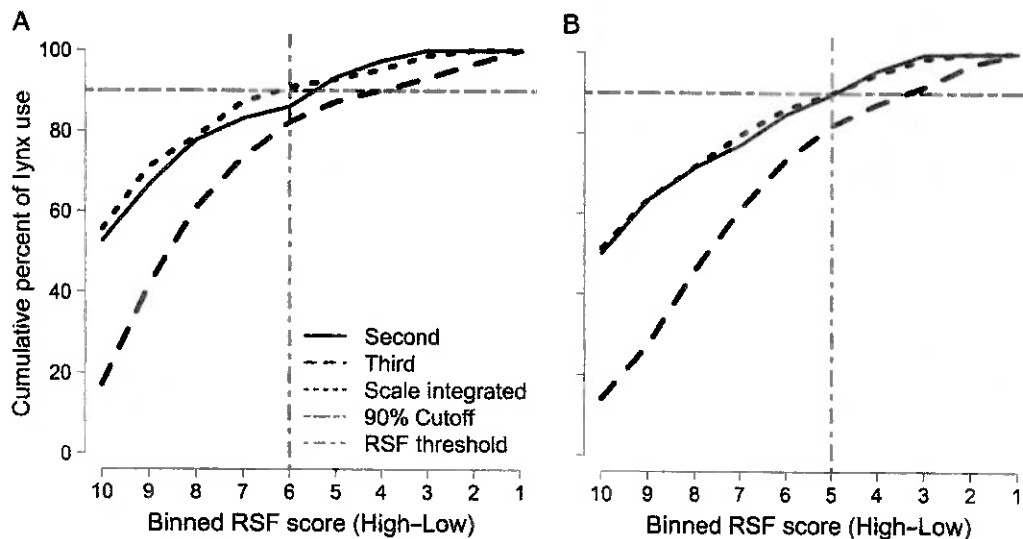


Fig. 4. Cumulative percent of withheld Canada lynx (*Lynx canadensis*) locations across our predicted probabilities of lynx use in western Montana, USA, using our second- and third-order, as well as scale-integrated, resource selection function (RSF) during winter (A; November–March) and summer (B; April–October). The x-axis represents 10 equal-area RSF scores ranging from high to low. The intersection of the “second,” “third,” and “scale-integrated” curves and the horizontal line indicate the RSF score that was required to capture 90% of lynx use. Because the RSF scores are of equal area (Boyce et al. 2002), these figures also illustrated that the scale-integrated RSF mapped more efficiently during winter (A) because it captured the same percent of lynx use over a reduced area (i.e., lower number of equal-area bins). The intersection of the vertical and horizontal lines illustrates an example of where managers could determine habitat vs. non-habitat using an empirically derived threshold from the mapped predictions.

(relative to random) of sparse and mature forest, respectively (Fig. 6, Table 6).

Finally, lynx exhibited functional responses in habitat use for predicted snowshoe hare habitat as well as vegetation cover. We observed a strong functional response for snowshoe hare occupancy and intensity of use for both sexes and across seasons (Fig. 7, Tables 5, 6). This indicated that habitat selection by lynx was strongest at low snowshoe hare availability and that selection decreased in strength as snowshoe hare availability increased (Fig. 7). In addition, females during winter demonstrated avoidance of Douglas-fir canopy cover at low availabilities but proportional use at higher availabilities (Table 5; Appendix S4). Males exhibited increasing habitat use with increasing availability of canopy cover of Douglas-fir during both seasons (Table 6; Appendix S4), as well as with increasing canopy cover of spruce-fir (although a slight decrease toward the maximum value) during winter and

lodgepole pine during summer (Table 6; Appendix S4). Males also demonstrated additive use (and consistent selection) for spruce-fir canopy cover and horizontal cover during the summer, as well as canopy cover of western larch during the winter (Table 6). All other relationships indicated proportional habitat use across sexes and seasons.

DISCUSSION

Translating the advancement of animal–habitat relationships to on-the-ground conservation is difficult and requires an integrated analytical framework. Here, we provided a process that merged the research motivation of understanding and prediction, as well as embraced the intricacies of exploring animal–habitat relationships. By examining habitat use, availability, selection, and functional responses, we were able to improve the current understanding of Canada

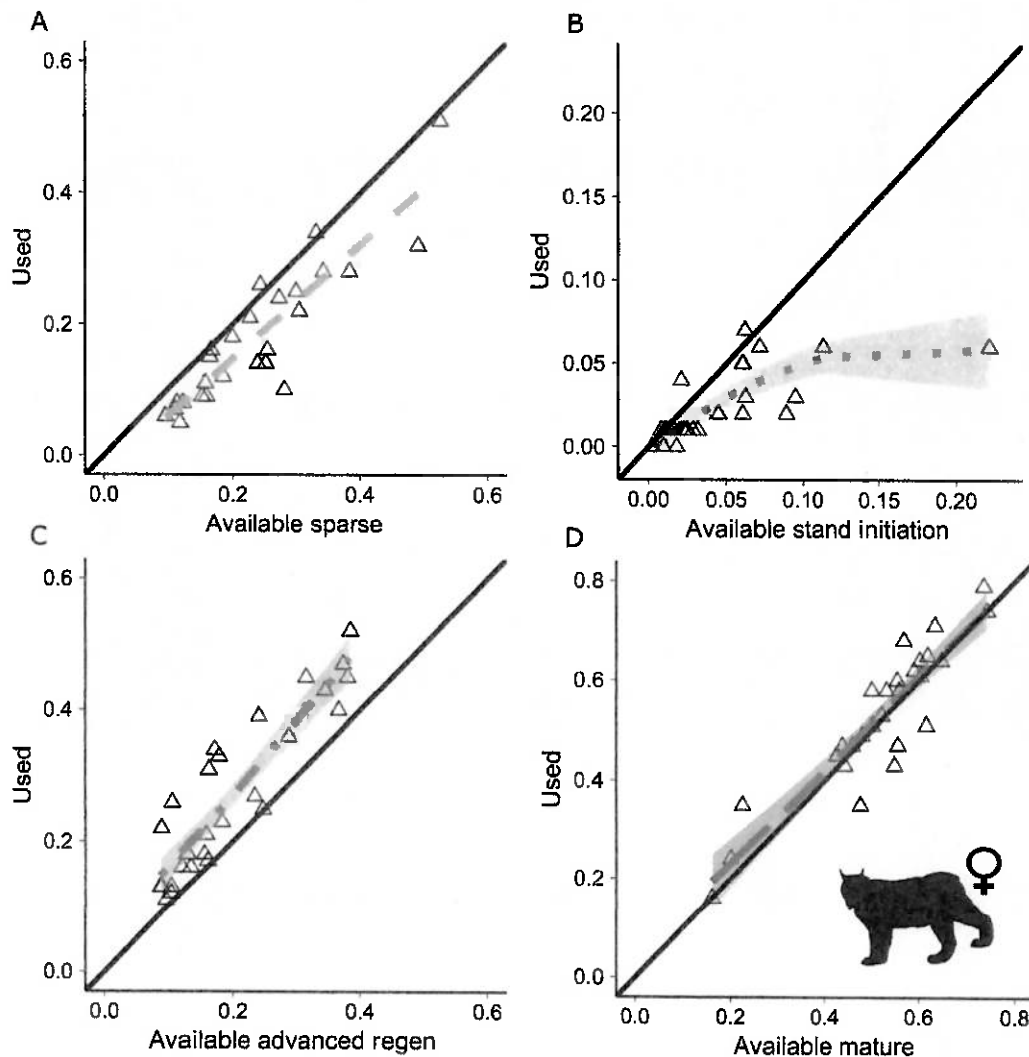


Fig. 5. Predicted relationships characterizing functional responses in habitat use by female Canada lynx (*Lynx canadensis*) during winter in western Montana, USA, across four forest structural stages. The diagonal line indicates random (i.e., proportional) habitat use. Data points indicate 27 female lynx used to develop predicted relationships and confidence bounds are 90% confidence intervals. Panels (A) and (B) indicate decreasing use, while panels (C) and (D) indicate additive use (and consistent selection) and proportional use, respectively. See Table 1 and Appendix S1 for details concerning forest structure classes.

lynx-habitat relationships while also providing maps predictive of lynx use. If we had not implemented all parts of our approach, we might have developed incomplete understandings of lynx-habitat relationships, which would result in incomplete conservation recommendations at best and misleading recommendations at worst. We illustrate this by presenting the following two examples.

We demonstrated that considering multi-scale habitat use and selection is essential when assessing animal-habitat relationships and developing conservation recommendations. Canada lynx in the Northern Rockies use a gradient of forest structures and compositions (Figs. 2, 3), but they use more mature, spruce-fir forest than any other structural stage or species. Contrasting these results with selection coefficients derived from

Table 5. Results from functional response analysis for female Canada lynx (*Lynx canadensis*) during winter (November–March) and summer (April–October) in western Montana, USA.

Covariate	Winter (n = 27 lynx)			Summer (n = 24 lynx)		
	β_0 (90% CI)	β_1 (90% CI)	R^2	β_0 (90% CI)	β_1 (90% CI)	R^2
PICO canopy cover	0.61 (−0.53 to 1.76)	0.99 (0.89–1.08)	0.92	0.62 (−0.32 to 1.56)	0.95 (0.87–1.03)	0.95
PIEN-ABLA canopy cover	0.66 (−1.44 to 2.75)	1.07 (0.97–1.18)	0.92	0.00 (−3.42 to 3.42)	1.01 (0.88–1.27)	0.80
LAOC canopy cover	1.29 (−0.57 to 3.14)	1.01 (0.74–1.28)	0.62	0.76 (−0.67 to 2.20)	0.99 (0.79–1.19)	0.77
PSME canopy cover	Second (P = 0.001)		0.96†	−0.46 (−2.80 to 1.89)	1.11 (0.88–1.33)	0.77
Horizontal cover	−0.27 (−6.12 to 5.58)	1.03 (0.92–1.13)	0.92	−1.14 (−11.27 to 9.00)	1.05 (0.86–1.23)	0.81
Sparse	−0.03 (−0.06 to 0.01)	0.87 (0.73–1.01)	0.82‡	−0.01 (−0.07 to 0.05)	0.95 (0.75–1.15)	0.76
Stand initiation	Second (P = 0.010)		0.61†	Second (P = 0.026)		0.60†
Advanced regeneration	0.05 (0.01–0.09)	1.12 (0.94–1.30)	0.82§	0.08 (0.02–0.15)	0.96 (0.60–1.32)	0.49§
Mature	0.04 (−0.04 to 0.12)	0.94 (0.79–1.09)	0.82	0.05 (−0.06 to 0.16)	0.81 (0.61–1.02)	0.68
Hare occupancy	Second (P = 0.002)		0.62†	0.35 (0.23–0.46)	0.53 (0.35–0.70)	0.55†
Hare intensity	1.30 (0.42–2.17)	0.69 (0.38–0.99)	0.37†	1.60 (0.81–2.39)	0.56 (0.26–0.86)	0.32†

Notes: CI, confidence interval. If a polynomial model was supported, we indicate the complexity of the model (i.e., second or third degree) and provide the P value of the likelihood-ratio test (χ^2 distribution). If a linear model was supported, we provide the estimated intercept (β_0) and slope (β_1) along with the 90% CI. For all models, we provide the coefficient of determination (R^2). Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

† Functional response.

‡ Perhaps biologically significant functional response, although not statistically significant ($\alpha \leq 0.10$).

§ Additive use (and consistent selection).

our most predictive RSFs (i.e., selected based on parsimony) highlighted the potential issues of solely relying on top RSFs for understanding habitat relationships. For instance, neither mature forest nor spruce-fir canopy cover were included in our most parsimonious RSF at the second order, despite the evidence that lynx exhibited selection for both of these resources (i.e., use greater than availability in Fig. 2). Moreover, our RSF models at the third order indicated comparatively weak selection for mature forest and spruce-fir canopy cover (Table 4). In fact, and consistent with previous work (Squires et al. 2010), lynx exhibited avoidance of mature forest in the summer (Table 4). Taken alone, our RSFs might lead one to suggest that Canada lynx are indifferent to the mature forest structure class (as suggested by others; Mowat and Slough 2003) and spruce-fir canopies. However, as previously mentioned, we demonstrated that mature, spruce-fir forests were used more by lynx than any other structure or species (Fig. 2). Because we summarized use and availability separately and across scales, we were able to highlight that (1) mature forests and spruce-fir canopies were highly available across our study area, potentially indicative of first-order selection processes and (2) it was indeed selection for mature, spruce-fir forests at

the second order (i.e., Fig. 2) that generated a context of broad availability at the third order. And by definition, it is difficult to strongly select habitat attributes that are abundant (Beyer et al. 2010, Kertson and Marzluff 2010). This example illustrates that characterizing use and availability prior to identifying predictive and parsimonious RSFs is essential for inferring covariate importance and that scale and availability are central to interpreting selection (as mentioned in Beyer et al. 2010, Matthiopoulos et al. 2011, Aarts et al. 2013, Northrup et al. 2013).

In addition, characterizing functional responses in habitat use allowed us to gain a deeper understanding of lynx–habitat relationships and provide land managers with expected responses under changing environmental conditions. For instance, during the winter (i.e., the most constraining season for lynx; Squires et al. 2010) female and male Canada lynx exhibited increasing and additive use, respectively, for advanced regenerating forest as it became more available (Fig. 6). In contrast, both sexes demonstrated decreasing use of stand initiation and sparse forest (Fig. 6). Placing these responses within their respective availability ranges (i.e., x -axis in Fig. 6) illustrated the magnitude of their effects, as well as indicated they are occurring within a broader

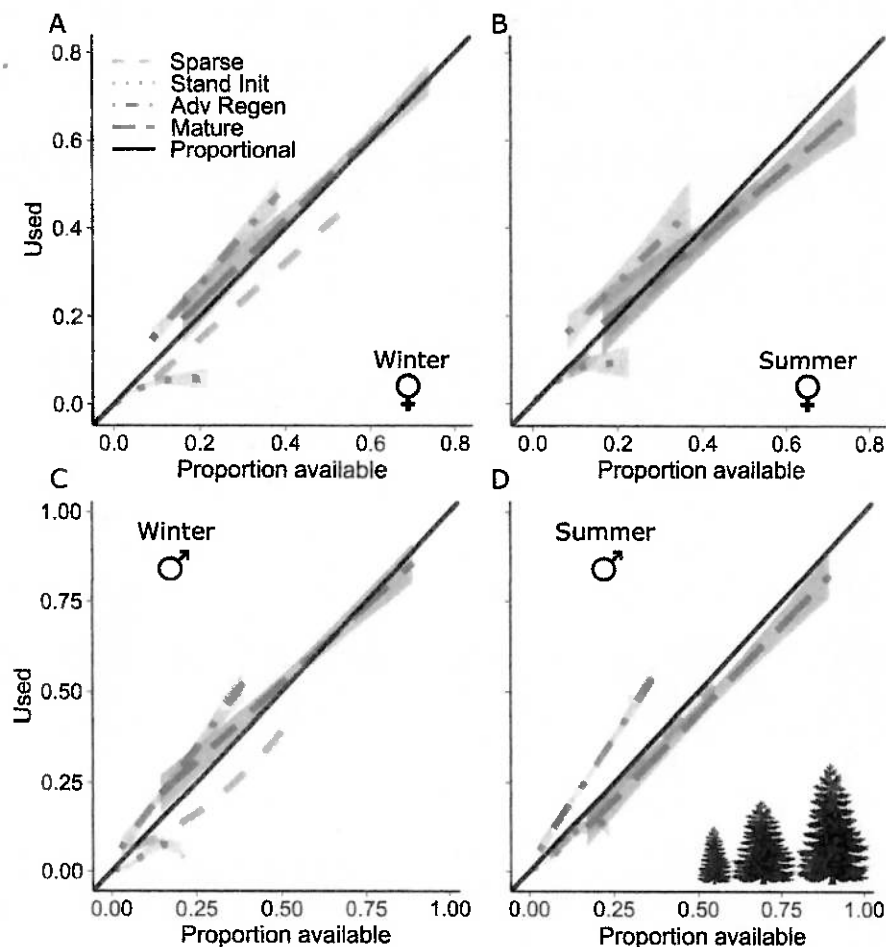


Fig. 6. Predicted relationships characterizing functional responses in habitat use by female (A: winter, and B: summer) and male (C: winter, and D: summer) Canada lynx (*Lynx canadensis*) in western Montana, USA, across four forest structural stages. The diagonal line indicates random (i.e., proportional) habitat use, and confidence bounds are 90% confidence intervals. Data points used to develop predicted relationships are not shown. See Table 1 and Appendix S1 for details concerning forest structure classes.

context of mature forest (Fig. 6). Interpreting functional responses within the appropriate context of availability is essential to avoid extrapolating third-order behavioral responses beyond the bounds set by second-order selection.

Moreover, these patterns capture some of the spatio-temporal issues land managers might consider when implementing landscape-altering actions to enhance lynx habitat. For example, managers might want to implement tools (e.g., timber harvest or fire) that create advanced regeneration in the long term, but recognize they will have to create stand initiation structures in

the short term. To dampen the negative response by lynx in the short term, managers might focus their conservation efforts in areas with relatively low availabilities of existing stand initiation or sparse forest. This example illustrates the applied insights and recommendations one can derive from examining functional responses. Landscape management can benefit greatly from the development of habitat maps (Johnson et al. 2004, Fattebert et al. 2015), but maps capture a spatio-temporal snapshot with no context as to how habitat use or selection might change with changing conditions (Hirzel and Le Lay 2008,

Table 6. Results from functional response analysis for male Canada lynx (*Lynx canadensis*) during winter (November–March) and summer (April–October) in western Montana, USA.

Covariate	Winter (<i>n</i> = 36 lynx)			Summer (<i>n</i> = 35 lynx)		
	β_0 (90% CI)	β_1 (90% CI)	R^2	β_0 (90% CI)	β_1 (90% CI)	R^2
PICO canopy cover	0.07 (−1.49 to 1.62)	1.05 (0.93–1.17)	0.86	−0.44 (−1.22 to 0.34)	1.07 (1.00–1.13)	0.96†
PIEN-ABLA canopy cover	Second (<i>P</i> = 0.002)		0.92†	2.35 (0.73 to 3.97)	0.95 (0.87–1.04)	0.91‡
LAOC canopy cover	1.28 (0.07 to 2.48)	1.03 (0.87–1.19)	0.78‡	0.83 (−0.07 to 1.74)	1.00 (0.87–1.13)	0.83
PSME canopy cover	−1.32 (−2.87 to 0.23)	1.20 (1.07–1.33)	0.88†	−1.02 (−2.26 to 0.22)	1.11 (1.00–1.21)	0.90†
Horizontal cover	3.19 (−2.25 to 8.63)	0.98 (0.88–1.08)	0.89	4.89 (0.71 to 9.06)	0.95 (0.88–1.03)	0.93‡
Sparse	Second (<i>P</i> = 0.015)		0.84†	−0.1 (−0.05 to 0.02)	0.97 (0.84–1.11)	0.82
Stand initiation	Third (<i>P</i> = 0.018)		0.52†	Third (<i>P</i> < 0.001)		0.82†
Advanced regeneration	0.03 (−0.01 to 0.06)	1.28 (1.09–1.46)	0.81†	0.02 (−0.01 to 0.05)	1.42 (1.26–1.59)	0.86†
Mature	0.09 (0.02 to 0.17)	0.86 (0.72–1.00)	0.76†	−0.04 (−0.12 to 0.05)	0.96 (0.81–1.12)	0.77
Hare occupancy	0.32 (0.23 to 0.41)	0.61 (0.48–0.74)	0.64†	Second (<i>P</i> = 0.015)		0.78†
Hare intensity	Second (<i>P</i> = 0.024)		0.80†	Second (<i>P</i> = 0.045)		0.85†

Notes: CI, confidence interval. If a polynomial model was supported, we indicate the complexity of the model (i.e., second or third degree) and provide the *P* value of the likelihood-ratio test (χ^2 distribution). If a linear model was supported, we provide the estimated intercept (β_0) and slope (β_1) along with the 90% CI. For all models, we provide the coefficient of determination (R^2). Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

† Functional response.

‡ Additive use (and consistent selection).

Matthiopoulos et al. 2011, Paton and Matthiopoulos 2016). Functional responses provide a means to assess animal responses to changing environments and as such are essential additions to characterizing habitat relationships (Moreau et al. 2012).

On advancing habitat relationships and conservation of Canada lynx

In this study, we expanded the current understanding of lynx–habitat relationships through our integrated analytical process. This combined analysis provided a refined lens of lynx resource use in the context of landscape pattern and conservation planning. For instance, we confirmed that Canada lynx in the Northern Rockies use a mixture of conifer species and structural stages, but highlighted that selection and use of mature, spruce–fir forests appears to be largely a first- or second-order process (Fig. 2). Additionally, lynx exhibited the strongest selection for intermediate snow depths, predicted snowshoe hare habitat, and lodgepole pine canopy cover at the second order of selection. These results emphasize the sensitivity of lynx to consistent and abundant snow as well as snowshoe hare availability. Previous work in the Northern Rockies has demonstrated that advanced regenerating or

multi-storied forests with a substantial component of lodgepole pine can provide high-quality habitat for snowshoe hares (Holbrook et al. 2017). Additionally, the reliance of snowshoe hares (Zimova et al. 2016) and lynx on snow conditions highlights foreseeable conservation challenges because snow extent and depth are projected to decrease within the Northern Rockies (Klos et al. 2014).

To our knowledge, all previous work on lynx–habitat relationships has implicitly assumed habitat use or selection will remain constant with changing availabilities (Poole et al. 1996, Squires et al. 2010, Simons-Legaard et al. 2013, Montgomery et al. 2014). Our work is the first to challenge that assumption. First, female lynx selected a narrower gradient of forest structures compared to males, and among-female use was most consistent during the most limiting season (i.e., winter R^2 > summer R^2 ; Table 5), whereas males did not display a similar pattern (Table 6). Thus, conservation planning should be focused on the needs of females when developing management plans. Second, both males and females demonstrated selection of predicted snowshoe hare occupancy and use, but selection increased as occupancy and use became less available (Fig. 7). This pattern was expected and consistent with

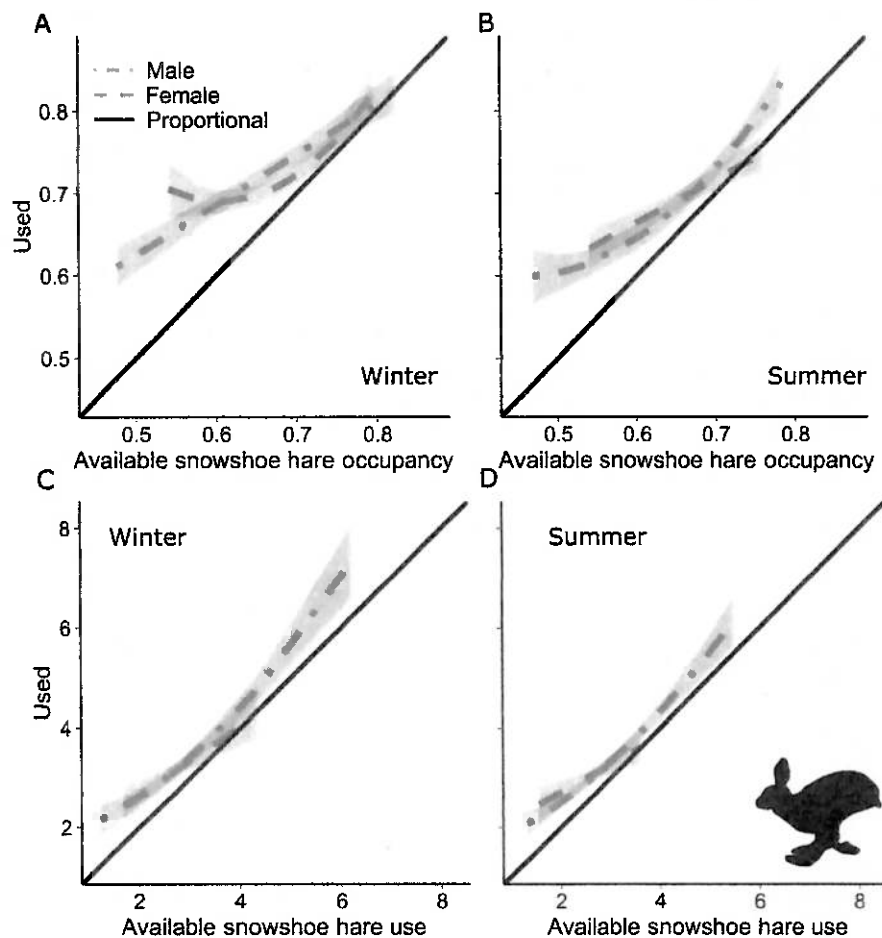


Fig. 7. Predicted relationships characterizing functional responses in habitat use by male and female Canada lynx (*Lynx canadensis*) in western Montana, USA, for snowshoe hare (*Lepus americanus*) occupancy (A: winter, and B: summer) and intensity of use (C: winter, and D: summer). The diagonal line indicates random (i.e., proportional) habitat use, and confidence bounds are 90% confidence intervals. Data points used to develop predicted relationships are not shown. See Table 1 for addition details on snowshoe hare covariates.

Canada lynx specializing on snowshoe hares (Elton and Nicholson 1942, Krebs et al. 2001, Ivan and Shenk 2016). Finally, male lynx demonstrated a positive functional response (increasing use with increasing availability) for advanced regeneration while females demonstrated additive use (Fig. 6). The affinity of lynx to advanced regenerating forest within a home range, coupled with the high use of mature forest (Fig. 3), suggests that Canada lynx spend a significant amount of time at the interface between mature and advanced regenerating forest. This is consistent with the mechanism that advanced

regeneration likely produces the highest snowshoe hare densities (Cheng et al. 2015), but the mature structure class is where hares are most accessible for lynx (Fuller et al. 2007, Ivan and Shenk 2016). This mechanism received demographic support by Kosterman (2014), who demonstrated that female lynx with core areas of highly connected mature forest and intermediate levels of regenerating forests had the highest probability of producing a litter. The integration of resource selection and functional response analyses begins to define the gestalt of landscape mosaics and behaviors that give rise to the

distribution of Canada lynx, which facilitates and informs habitat conservation efforts.

The second motivation for this work was to provide efficient habitat maps for Canada lynx with the goal of assisting land managers in their decision-making processes. Managers of public lands are tasked with making multi-scale decisions in the context of social, biological, and legal complexities and thus require objective and science-based designations of habitat for species listed under the ESA, SARA, or similar statutes. We provided five landscape-level maps characterizing the probability of use by Canada lynx in the Northern Rockies (Fig. 3), all of which were deemed predictive of lynx use (Fig. 4). Although, consistent with DeCesare et al. (2012), our scale-integrated habitat maps appeared to perform best based on validation and mapping efficiency (Fig. 4). We believed this was the case because the second-order map had a much wider range in relative probabilities of use (i.e., more discriminatory) than the third-order map, such that a high prediction from the third order would seldom override the second order except on the low end of the second-order range. Therefore, by integrating the second order with the third order, the scale-integrated map appears to capture the hierarchical nature of habitat selection and generate efficient maps. Finally, by extending the concept of Boyce et al. (2002) we provided a simple, objective, and defensible approach to determine the threshold value of a habitat map (Fig. 4). This will be helpful for land managers if they are required to make decisions in a binary fashion, where a habitat and non-habitat designation is needed.

The application of our habitat maps, or the data characterizing lynx habitat, will depend on the extent and resolution of the management objective. For instance, our second-order and scale-integrated habitat map would be best applied at broad extents (e.g., landscape level). At the project level (e.g., 40 acres or 16 ha), however, the third-order derived maps would likely be the most informative for land managers, but this is conditioned on the project area occurring within lynx habitat as modeled at the broad extent. At fine resolutions (3–10 acres or 1–4 ha), managers will likely need to couple our maps with site visits (and field data described elsewhere; Squires et al. 2010) to develop the most informed decisions concerning Canada lynx habitat.

Similarly, the absolute values of forest structure and composition characterizing lynx habitat (e.g., as in Fig. 2, Table 2; Appendices S1 and S3) should be applied in a relative and general sense. All of our metrics are derived from models with error and characterize resolutions $\geq 100 \text{ m}^2$ (Table 1). Indeed, maps of forest characteristics and animal habitat are useful tools for conservation planning and prioritization (Johnson et al. 2004, DeCesare et al. 2012), but will likely need refinement based on site-specific understandings derived from direct observation.

CONCLUSIONS

Understanding and predicting habitat is essential in animal ecology and management (Elith and Leathwick 2009), particularly for species that are threatened or endangered. Here, we demonstrated an integrated process to understand, prioritize, and predict habitat, which we applied in the case of the federally threatened Canada lynx. Our approach was novel because we characterized habitat use, availability, selection, and functional response across scales, which embraced the multi-scale behavioral process of habitat selection (Johnson 1980, Boyce 2006, Meyer and Thuiller 2006). Although previous work has demonstrated the conditional nature of habitat selection, and the potential issues deriving importance from selection (Beyer et al. 2010, Anderson et al. 2012, Northrup et al. 2013), our work is among the first to highlight the conservation costs of such issues. This is particularly a concern when examining a subset of Johnson's (1980) orders of selection, which is commonly the case. Further, we developed a synthetic approach to characterize functional responses in habitat use, which provided critically important insights into the behavior of Canada lynx. Indeed, assessing functional responses in habitat use can inform both ecologists and managers on the expected responses of animals to changing environmental conditions and thus should become basic tools in applied ecology (Moreau et al. 2012). Successful conservation efforts for most endangered and threatened species require spatial characterizations of habitat and precise understandings of the mechanisms giving rise to those spatial depictions. Our multi-scale and integrated process offers a means to that end.

Multiscale habitat relationships of snowshoe hares (*Lepus americanus*) in the mixed conifer landscape of the Northern Rockies, USA: Cross-scale effects of horizontal cover with implications for forest management

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Abstract

Snowshoe hares (*Lepus americanus*) are an ecologically important herbivore because they modify vegetation through browsing and serve as a prey resource for multiple predators. We implemented a multiscale approach to characterize habitat relationships for snowshoe hares across the mixed conifer landscape of the northern Rocky Mountains, USA. Our objectives were to (1) assess the relationship between horizontal cover and snowshoe hares, (2) estimate how forest metrics vary across the gradient of snowshoe hare use and horizontal cover, and (3) model and map snowshoe hare occupancy and intensity of use. Results indicated that both occupancy and intensity of use by snowshoe hares increased with horizontal cover and that the effect became stronger as intensity of use increased. This underscores the importance of dense horizontal cover to achieve high use, and likely density, of snowshoe hares. Forest structure in areas with high snowshoe hare use and horizontal cover was characterized as multistoried with dense canopy cover and medium-sized trees (e.g., 12.7–24.4 cm). The abundance of lodgepole pine (*Pinus contorta*) was associated with snowshoe hare use within a mixed conifer context, and the only species to increase in abundance with horizontal cover was Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Our landscape-level modeling produced similar patterns in that we observed a positive effect of lodgepole pine and horizontal cover on both occupancy and use by snowshoe hares, but we also observed a positive yet parabolic effect of snow depth on snowshoe hare occupancy. This work is among the first to characterize the multiscale habitat relationships of snowshoe hares across a mixed conifer landscape as well as to map their occupancy and intensity of use. Moreover, our results provide stand- and landscape-level insights that directly relate to management agencies, which aids in conservation efforts of snowshoe hares and their associated predators.

KEYWORDS

gradient modeling, habitat selection, habitat use, occupancy, quantile regression, Random Forest

use pellets as a measure of intensity of use. We visited our sampling locations only once; therefore, we did not estimate detection probabilities for occupancy (sensu MacKenzie et al., 2002). However, it is unlikely that the detection probability was substantially less than one because we surveyed small and spatially defined areas (5.1×305 cm subplots) for snowshoe hare pellets rather than surveying for the animal itself. Because of the small area we surveyed within each 20×20 m plot, we interpreted our measure of snowshoe hare occupancy as conservative (i.e., false positives < false negatives). Finally, we assumed that potential differences in decay rates of pellets among habitats (e.g., Prugh & Krebs, 2004) was a relatively random source of error given the spatial extent of our analysis (i.e., 3.6 million ha).

2.3 | Landscape-scale environmental data

We considered a suite of vegetative, topographic, and climate variables, which we hypothesized would influence snowshoe hare occupancy and intensity of use (Table 1). We used percentage canopy cover for five conifer species (from Savage et al., 2015): lodgepole pine, western larch, Douglas-fir, subalpine fir, and Engelmann spruce. Previous work indicated a positive relationship between snowshoe hares and spruce-fir habitats (e.g., Berg et al., 2012; Ivan, White, & Shenk, 2014), and thus, we added a spruce-fir variable to our suite. Second, we used Landfire Existing Vegetation Cover (EVC; LANDFIRE, 2012) data to calculate proportion of nonforested areas (i.e., naturally open, burns, timber harvests) as well as edge density, both of which could exhibit a negative or parabolic relationship with snowshoe hare occupancy and intensity of use (e.g., Griffin & Mills, 2009; Lewis et al., 2011; Thornton et al., 2013). Proportion of nonforest (nonforest includes open areas as well as sparse trees) and edge density were both based on a forest versus nonforest classification, which we defined as <40% canopy cover of trees within the Landfire EVC dataset. Photointerpretation confirmed that this decision was the most appropriate boundary for dense forest versus sparse to nonforest (we assessed multiple thresholds between 30 and 60%). We also used the potential vegetation groupings compiled by Region 1 of the USDA Forest Service (Milburn, Bollenbacker, Manning, & Bush, 2015) to calculate the proportion of area within cool and wet spruce-fir potential vegetation types. Finally, we used Landsat TM images from summer 2011 (see Savage et al., 2015 for image processing details) to calculate the Normalized Difference Vegetation Index (Pettorelli et al., 2005) as well as the tasseled cap vegetation indices (Huang, Wylie, Yang, Homer, & Zylstra, 2002). Tasseled cap metrics include brightness, greenness, and wetness, which indicate soil reflectivity, amount of green vegetation, and amount of soil and vegetation moisture, respectively. We generally expected a positive relationship between green vegetation and snowshoe hares and a negative relationship between snowshoe hares and particularly open and wet locations (i.e., high values of brightness and wetness).

To characterize topography, we calculated derivatives of a digital elevation model (National Elevation Dataset, USGS). We computed slope, topographic roughness (Jenness, 2004), a heat load index

(McCune & Keon, 2002), a topographic position index (Guisan, Weiss, & Weiss, 1999), and a compound topography index (Gessler, Moore, McKenzie, & Ryan, 1995). Our heat load index, topographic position index, and compound topography index represented hot-dry to cool-moist areas, relative concavity or convexity, and amount of water accumulation, respectively. We expected snowshoe hares to be associated with cool-moist areas with intermediate water accumulation in the context of concave topographic locations (e.g., basins vs. ridges). All topographic metrics were calculated using either DEM Surface Tools for ArcGIS (Jenness, 2013) or Geomorphometric and Gradient Metrics Toolbox (Evans, Oakleaf, Cushman, & Theobald, 2014) within ArcGIS (ESRI, 2011).

Lastly, because of the relationship between snowshoe hares and snow (e.g., Mills et al. 2013, Sultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016), coupled with the sensitivity of snow depth and extent to warming temperatures (Barnett, Adam, & Lettenmaier, 2005), we gathered spatially explicit data for snow depth from the Snow Data Assimilation System (SNODAS) within the National Operational Hydrologic Remote Sensing Center (NOHRSC, 2004). Previous analyses indicated a strong association between SNODAS-derived estimates of snow depth and field measurements in the forested systems of the Northern Rockies (Clow, Nanus, Verdin, & Schmidt, 2012). We downloaded 1 April snow depth for 2012–2013 and averaged across years to produce a mean estimate for our study area. We expected a parabolic relationship between snow depth and snowshoe hares because hares occupy subalpine environments (vs. high-elevation alpine areas with deeper snow, and low-elevation areas with little snow; elevation-snow depth $r = .70$) in the Northern Rockies.

2.3.1 | Horizontal cover mapping

Nearly all previous studies of snowshoe hare habitat relationships indicated a strong relationship with horizontal cover (Hodges, 2000a, 2000b). Thus, we sought to develop a new spatial map explicitly characterizing horizontal cover, which we could then use in our landscape-level modeling of snowshoe hares (see Section "2.5"). Previous analyses within our study area indicated that horizontal cover is strongly associated with subalpine fir (Squires et al., 2010). Consequently, as spatial covariates for our model to map horizontal cover, we used the species-specific canopy cover layers for the five dominant conifers within our study area (Savage et al., 2015), along with a stack of 22 Landsat bands and derived spectral components and 2 NAIP texture images (see Savage et al., 2015 for stack details), and four topographic metrics. The topographic metrics included a digital elevation model (National Elevation Dataset, USGS), slope, heat load index (McCune & Keon, 2002), and a compound topographic index (Gessler et al., 1995).

We built a Random Forest (RF) model (Breiman, 2001; Cutler et al., 2007) to evaluate our ability to spatially predict horizontal cover across our study area. Our sample size was 1,275 plots with a 70%–30% allocation among training and testing data, respectively. We used 1,275 because, based on photointerpretation, they were homogenous

non-forest
40%
= forest

(<1,000 m; Griffin & Mills, 2009) of snowshoe hares. To begin our modeling process, we first ran separate RF models for each scale-variant covariate (all except snow depth, which was only available at the coarsest scale evaluated; Table 1) to determine the most important scale as measured by the mean decrease in accuracy (Cutler et al., 2007). Next, we compiled all covariates at the most influential scale (Table 1) and removed those that were collinear ($|r| > .75$; Table 1). We then built our RF model with 5,000 bootstrapped trees and implemented a covariate selection procedure described by Murphy, Evans, and Storer (2010), whereby we assessed the trade-off in number of covariates and predictive ability across thresholds of model improvement ratios between 0.1–1 by 0.1 increments. We selected the model with the fewest covariates that maintained the highest predictive performance. We then assessed model fit of the classification model by reporting the “out-of-bag error” (OOBE), classification error among classes (i.e., unoccupied and occupied), and the predicted probabilities of occupancy for occupied and unoccupied plots. We assessed fit of the regression model using the RF R^2 , root mean square error (RMSE), and assessing the correlation between observed and predicted values. For both models, we assessed model significance by randomizing the response (i.e., occupancy or intensity of use), calculating the OOBE or R^2 of each model ($n = 1,000$), and determining whether the observed value (OOBE or R^2) from our built model was >95th percentile of the randomized values ($p < .05$), which indicates a significant model (Murphy et al., 2010). We then graphed the effects of our selected covariates on occupancy and intensity of use using partial dependence plots (Cutler et al., 2007). Finally, to help guide conservation efforts, we generated a predicted map of occupancy and intensity of use for snowshoe hares throughout our study area and assessed how both metrics were distributed across protected areas (i.e., Glacier National Park and wilderness; Figure 2) and multiple-use lands. Specifically, we estimated the area of predicted occupancy and the mean predicted

pellet density (i.e., pellets/5.1 × 305 cm subplots) within both areas. All landscape-scale analyses were performed in ArcGIS (ESRI, 2011) or R (R Core Team 2015) using the “randomForest” (Liaw & Wiener, 2002), “rfUtilities” (Evans & Cushman, 2009), and “raster” (Hijmans, 2015) packages.

3 | RESULTS

Across our sample of plots, the number of trees ≥ 12.7 cm in DBH was distributed among Douglas-fir (29%), lodgepole pine (20%), Engelmann spruce (15%), western larch (15%), and subalpine fir (14%); other species made up the remaining 8%. We determined that 67% of the plots were occupied by snowshoe hares as indexed by pellet counts (33% were unoccupied). We observed a range of 0–40.4 ($\bar{x} = 2.36$) snowshoe hare pellets/5.1 × 305 cm subplot. For comparative purposes (e.g., Hodges et al., 2009; Mills et al., 2005), we applied the equation of Krebs, Boonstra et al. (2001) to the mean value within our categories of nonzero pellet densities (i.e., 0.2–1.2, 1.2–2.4, 2.4–5.2, and 5.2–40.4 pellets/subplot) to estimate a range of hare densities within our study area. Although our estimates might be biased high because our plots were not precleared, we nevertheless found that snowshoe hare densities were 0.28, 0.81, 1.48, and 4.21 hares/ha across our classes of pellet density, respectively. Our overall estimate (i.e., across all samples including zeros) was 1.01 snowshoe hares/ha.

3.1 | Plot scale

Occupancy and intensity of use by snowshoe hares were positively related to horizontal cover (Figure 4). Our logistic model indicated that the odds of snowshoe hare occupancy increased by 20% for every 10% increase in horizontal cover (z -value = 7.87, $df = 1,295$,

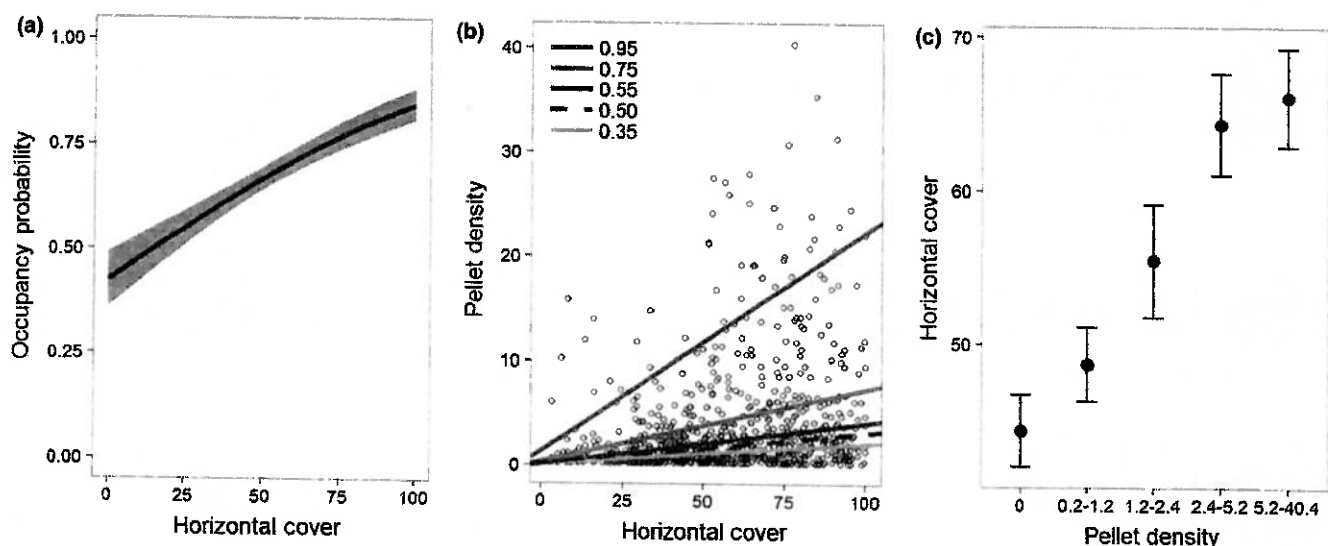


FIGURE 4 (a) Predicted occupancy ($\pm 95\%$ CI) of snowshoe hares (*Lepus americanus*) as a function of horizontal cover. (b) Relationship between pellet density of snowshoe hares and horizontal cover for five quantiles of the pellet density distribution ($\tau = 0.35, 0.50, 0.55, 0.75$, and 0.95). The black and dashed line indicates the median value (i.e., 0.50). (c) Mean ($\pm 95\%$ CI) horizontal cover across the distribution of pellet densities

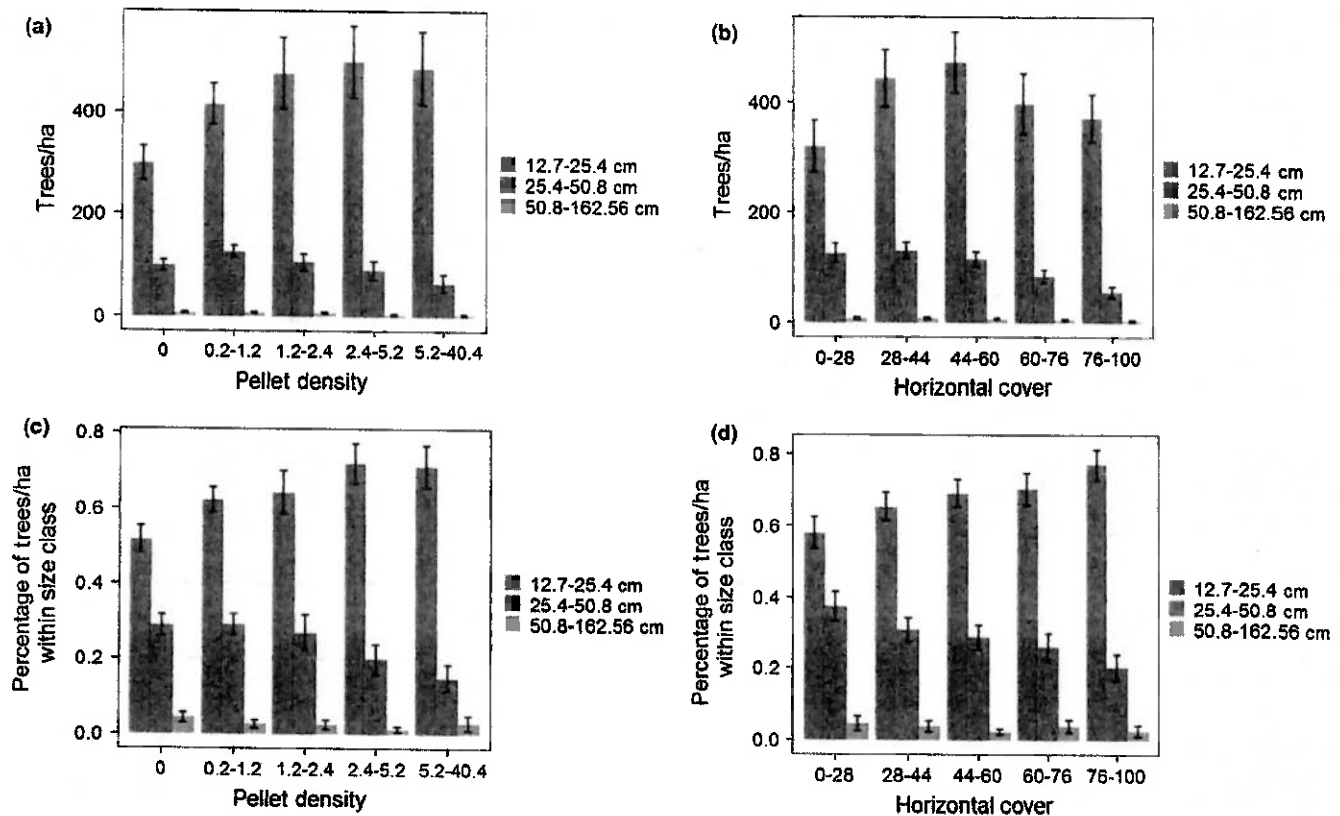


FIGURE 7 Mean ($\pm 95\%$ CI) trees/ha within size classes across the distribution of snowshoe hare (*Lepus americanus*) pellet density (a) and horizontal cover (b). Mean percentage ($\pm 95\%$ CI) of trees/ha within size classes across the distribution of pellet density (c) and horizontal cover (d). All metrics were calculated using the Forest Vegetation Simulator (Crookston & Dixon, 2005) from data collected using a 10 basal area factor prism, and only included trees ≥ 12.7 cm (i.e., 5 inches) in DBH

snowshoe hares and offers specific insight for forest management and snowshoe hare conservation.

4.1 | Plot-scale patterns

Previous work has identified a positive relationship between snowshoe hare density and horizontal cover as well as spruce-fir and lodgepole pine forests (Berg et al., 2012; Cheng et al., 2015; Hodges et al., 2009; Ivan et al., 2014; Koehler, 1990). Our data support these conclusions; however, the interpretation of our results is more nuanced. Our analyses highlighted that the abundance of spruce-fir is more associated with horizontal cover than any other species of conifer (Figures 6 and 8), and we found that horizontal cover was strongly associated with occupancy and intensity of use by snowshoe hares (Figure 4). However, we did not discover any consistent relationship between snowshoe hare occupancy or intensity of use and spruce-fir per se (although see parabolic relationships in Figure 5). Thus, our data suggest that horizontal cover is an important attribute influencing snowshoe hares and that this attribute is associated with forests that have a substantial spruce-fir component (relative to those without a spruce-fir component). Preserving the horizontal cover that spruce-fir trees provide within the mixed conifer context of the Northern Rockies will likely be important for the conservation of snowshoe hares.

Moreover, we found a species-specific association between snowshoe hares and abundance of lodgepole pine, which we attributed mostly to nutritional mechanisms. Ellsworth et al. (2013) discovered that lodgepole pine produced higher levels of digestible protein than other common conifers in the Northern Rockies (e.g., Douglas-fir, subalpine fir, Engelmann spruce, western larch) and that overwinter depletion of biomass and browsing by snowshoe hares was most associated with lodgepole pine. Although our data indicate that areas with high use by snowshoe hares are indeed highly mixed conifer forests (e.g., Figure 5), forest managers within our study region could use lodgepole pine as well as spruce-fir, or more specifically horizontal cover, as initial indicators of potential snowshoe hare habitat.

Our results reinforced previous studies highlighting the importance of dense forests for snowshoe hares (e.g., Berg et al., 2012; Griffin & Mills, 2007; Hodges et al., 2009; Hodson et al., 2011; Ivan et al., 2014; Lewis et al., 2011). Our data indicated that dense horizontal cover within multistoried forests with a substantial component of medium-sized trees (i.e., 12.7–25.4 cm) produced the highest use by snowshoe hares, which was also found in previous studies within Montana (Griffin & Mills, 2007), Washington (Koehler, 1990; Lewis et al., 2011), Wyoming (Berg et al., 2012; Hodges et al., 2009), and Colorado (Ivan et al., 2014). Results from our data support conclusions similar to previous studies in that disturbing (e.g., cutting or burning) multistoried forests with high stem densities (particularly in the

5-10"
down

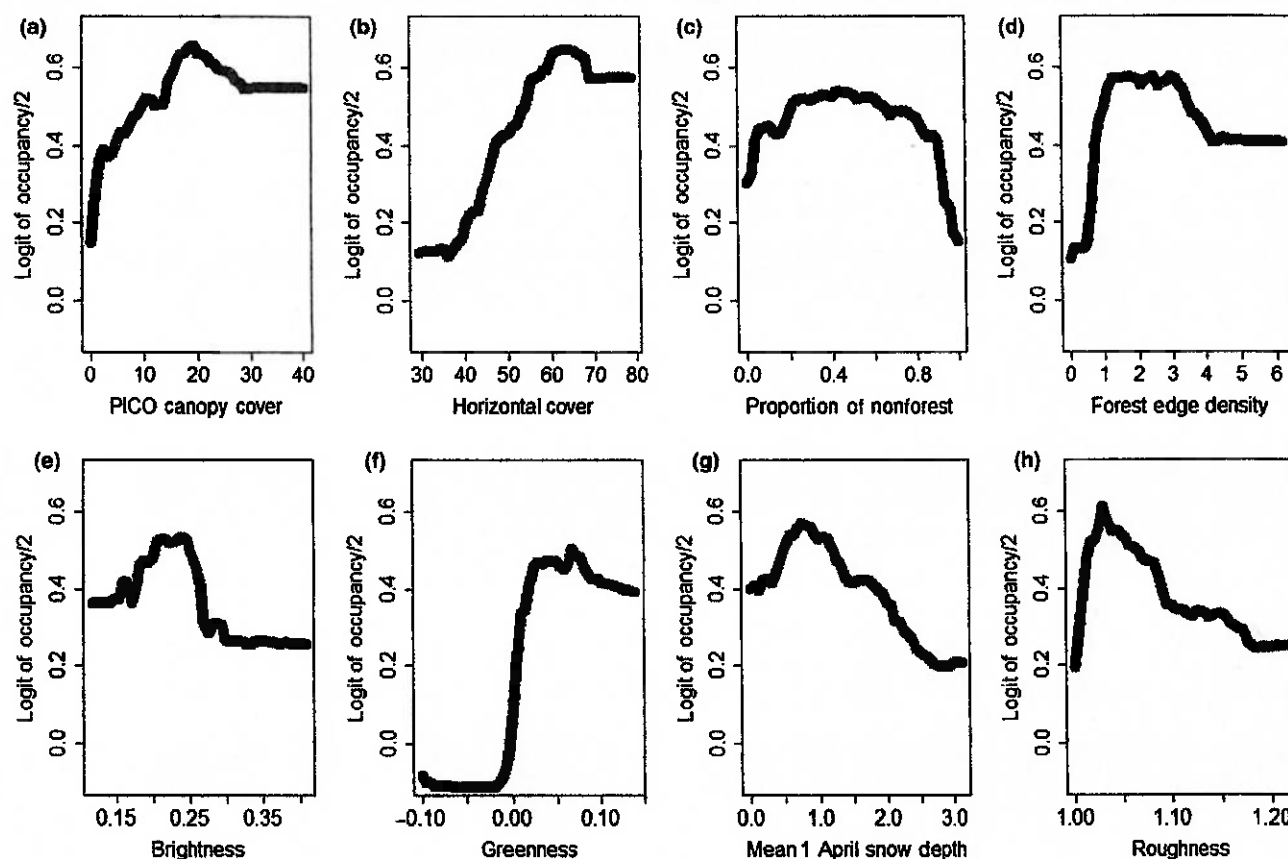


FIGURE 9 Partial dependence plots displaying the relationship between occupancy probability of snowshoe hares (*Lepus americanus*) and the covariates (a–h) that exhibited a consistent trend from our top Random Forest model. See Table 1 for covariate descriptions

because this landscape is projected to experience substantial changes via reduction in snow (e.g., Klos et al., 2014; McKelvey et al., 2011) and increased wildfire (Liu et al., 2013; Stavros et al., 2014).

Of the few studies on snowshoe hares that have been conducted at a landscape level, results indicated that occupancy is positively associated with vegetation cover, snow cover, and surrounding population density (Saultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016; Saultaire, Pauli, Martin, Meyer, Notaro, et al., 2016; Thornton et al., 2013). Furthermore, Lewis et al. (2011) highlighted that vegetation cover at the local and neighborhood level was important for density of snowshoe hares. Our occupancy results support the notion that vegetation cover and perhaps moisture content are important for snowshoe hares in that we observed a positive relationship between occupancy and canopy cover of lodgepole pine, horizontal cover, and tasseled cap greenness and wetness. Snow depth, however, was the most important variable characterizing occupancy of snowshoe hares, which supports the recent findings of Saultaire, Pauli, Martin, Meyer, & Zuckerberg (2016) and Saultaire, Pauli, Martin, Meyer, Notaro, et al. (2016) indicating that snow cover is more important than forest cover for characterizing snowshoe hare occupancy. In addition, we discovered that occupancy of snowshoe hares was associated with relatively flat topography, and perhaps some level of disturbance at a coarse resolution. Although canopy and horizontal cover are clearly important, our results suggest that some open areas (e.g., edges) within a matrix of high-quality cover provide resources for increased use by

snowshoe hares. Finally, similar to occupancy, the intensity of use by snowshoe hares exhibited a positive relationship with canopy cover (both lodgepole and western larch) and horizontal cover. We attributed the positive effect of lodgepole pine to similar nutritional mechanisms aforementioned (e.g., Ellsworth et al., 2013). However, the positive effect of western larch appeared to be related to a broad-scale productivity gradient in that western larch tended to occur only in multiple-use lands (vs. wilderness and national parks), and was most abundant in the northwestern portion of our study area (i.e., considered most productive). We observed a negative effect of Douglas-fir on intensity of use by snowshoe hares, which was expected given the low level of horizontal cover associated with stands dominated by Douglas-fir (Figures 6 and 8). The positive effect of tasseled cap brightness and a negative effect of greenness are consistent with the hypothesis that a few open areas (e.g., edges) within a matrix of high-quality cover could provide additional foraging opportunities for snowshoe hares. This hypothesis is supported by previous work indicating that foraging behavior by snowshoe hares was largely associated with food supply (e.g., Ellsworth et al., 2013; Hodges & Sinclair, 2005), and not simply driven by predation risk.

4.3 | Foreseeable conservation challenges

Our work also highlighted the foreseeable challenges facing decision makers that are related to climate-induced reductions in snow depth

structure (e.g., more stand initiation and regeneration) and species composition (e.g., increase in fire-adapted species such as lodgepole pine). Previous work has indicated a positive response of snowshoe hares to fire (e.g., Cheng et al., 2015; Hodson et al., 2011), but there is a temporal delay, suggesting that the unburned matrix surrounding fires might be critically important in the short term (e.g., Abele et al., 2013; Ausband & Baty, 2005; Lewis et al., 2011). These broad-scale changes suggest that forest management for snowshoe hare habitat will likely be a nuanced and landscape-level endeavor.

Additionally, perhaps of equal concern are the indirect effects associated with changes induced by snow reduction and increased wildfire. For example, predation is the main process driving population dynamics of snowshoe hares (Feierabend & Kiehl, 2015; Krebs, 2011; Wirsing et al., 2002), and changes in snow, or vegetation structure due to fire, could introduce or remove predators. These indirect effects might be of more concern in the southern range of snowshoe hares because densities tend to be lower than the northern range and the landscapes are generally more fragmented (Hodges et al., 2009; Thornton et al., 2013; Wirsing et al., 2002), perhaps making the persistence of southern populations more vulnerable to changes. Understanding the consequences of landscape-scale changes such as climate and wildfire on the distribution, density, and demography of snowshoe hares and their predators will continue to be important for wildlife conservation in northern North America.

5 | CONCLUSIONS

Our gradient-based (vs. type-based) and multiscale approach embraced the current paradigm in ecology (e.g., Cushman et al., 2010; McGill, 2010) and advanced the understanding and management of snowshoe hare habitat. First, our analyses produced consistent patterns across scales and emphasized the importance of horizontal cover, spruce-fir, and lodgepole pine as indicators of hare habitat within the mixed conifer context of the Northern Rockies. Second, we predicted snowshoe hare habitat and demonstrated that it is patchily distributed at a coarse scale within the Northern Rockies and that multiple-use lands (e.g., national forests, state-managed lands) are essential for the conservation of snowshoe hare habitat. Simply focusing on wilderness areas or national parks for conservation of snowshoe hares will likely result in ineffective strategies. Third, we provided explicit structural information concerning snowshoe hare habitat within the mixed conifer forests of the Northern Rockies that can be directly implemented by forest managers. The structure of forests with high use by snowshoe hares was characterized as dense (particularly in the understory), relatively closed, and multistoried, which we described using metrics such as quadratic mean diameter, trees/ha, canopy cover, and basal area (for additional metrics, see Table 2 and Table A1 in Appendix A). These stand characteristics can arise in nearly all successional stages and are presumably realized following disturbance agents (e.g., wildfire, insect damage, root disease, or cutting) of intermediate severity that allow patches of light to reach the forest floor. Overall, forest managers can apply this collective understanding to

inform decision making relevant to habitat management of snowshoe hares and their associated predators within the Northern Rockies.

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CONFLICT OF INTEREST

None declared.

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Spatio-temporal responses of Canada lynx (*Lynx canadensis*) to silvicultural treatments in the Northern Rockies, U.S.

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ABSTRACT

Forest managers are often tasked with balancing opposing objectives, such as altering forest structure and conserving forest-dwelling animals. Consequently, to develop holistic strategies managers require information on how forest manipulations influence species of conservation concern, particularly those that are federally threatened or endangered. Here, we characterized how differing silvicultural treatments ($n = 1,293$ – forest thinnings; removal of small trees, selection cuts; trees harvested in small patches, and regeneration cuts; clearcuts of nearly all trees) influenced the resource use of a threatened forest carnivore, Canada lynx (*Lynx canadensis*), over a temporal gradient of 1–67 years after treatment. To do this, we used an extensive GPS dataset on 66 Canada lynx (i.e., 164,593 locations) collected during 2004–2015 within the Northern Rocky Mountains, U.S. We used univariate analyses and hurdle regression models to evaluate the spatio-temporal factors influencing lynx use of treatments. Our analyses indicated that Canada lynx used treatments, but there was a consistent cost in that lynx use was low up to ~10 years after all silvicultural actions. However, cumulative use (in both winter and summer) by lynx reached 50% at ~20 years after a thinning treatment, whereas it took ~34–40 years after a selection or regeneration cut. This indicated that Canada lynx used thinnings at a faster rate post-treatment than selection or regeneration cuts, and that lynx used selection and regeneration cuts in a similar fashion over time. Further, we discovered that lynx occupancy and intensity of treatment use was influenced by the composition of forest structure in the surrounding neighborhood. In some instances, the existing forest structure surrounding the treatment and the time since treatment interactively influenced lynx use; a pattern characterizing a spatio-temporal functional response in habitat use. This demonstrated that both the recovery time as well as the spatial context of a particular area are important considerations when implementing different silvicultural treatments for Canada lynx at the landscape scale. For example, if a selection cut was implemented with abundant mature, multi-storied forest (i.e., a preferred habitat by lynx) in the surrounding landscape, lynx would use these treatments less over time than if the neighborhood contained less mature forest. Forest managers can apply our spatio-temporal understandings of how lynx respond to forest silviculture to refine expectations and develop strategies aimed at both forest management and the conservation of Canada lynx.

1. Introduction

Forest managers, and in particular those of public lands, are increasingly faced with the challenge of balancing opposing objectives. For instance, in the forests of North America a pervasive challenge is the conservation of threatened and endangered species that rely on complex forest structures, while simultaneously managing disturbance

(e.g., wildfire risk, bark beetle outbreaks) or forest products through silviculture (e.g., Zielinski et al., 2013; Stephens et al., 2014; Tempel et al., 2014; Sweitzer et al., 2016). Unfortunately, the difficulty of navigating these issues has only increased in recent decades given the increase in forest disturbances such as wildfire and bark beetle outbreaks (e.g., Westerman et al., 2006; Bentz et al., 2010; Jones et al., 2016). Balancing species conservation and managing forest

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2.2. Silvicultural treatments, surrounding forest structure, and treatment use by Canada lynx

2.2.1. General overview of analysis

Our main objective was to characterize how time since treatment, treatment type, and surrounding forest structure influenced treatment use by Canada lynx. Given the diversity of silvicultural treatments within lynx home ranges, we first developed an ecologically-based framework to stratify treatments. We used the U.S. Forest Service's FACTS (Forest Activity Tracking System) database and a time-series (1972–2014) of the Normalized Burn Ratio (NBR), a variable created from the Landsat archive using the near infrared (NIR) and shortwave infrared (SWIR) bands (i.e., $NBR = NIR - SWIR / NIR + SWIR$), to identify distinct silvicultural treatments and evaluate the response of vegetation as a function of time since treatment. The NBR is similar to the Normalized Difference Vegetation Index ($NDVI = NIR - Red / NIR + Red$), but previous work has demonstrated that NBR outperforms NDVI when assessing differences in vegetation impact (e.g., Escuin et al., 2008; Harris et al., 2011). For instance, the gradient of the NBR was 1.6–2.3 times wider than the gradient of NDVI for the same areas impacted by wildfire (Escuin et al., 2008; Harris et al., 2011), which highlighted the increased resolution of the NBR to discern differences in vegetation responses. Therefore, we used the NBR to validate our treatment stratification from FACTS, which we expected to capture a gradient in vegetation impact. We then used this stratification, along with univariate analyses and hurdle regression models (Mullahy, 1986; Zeileis et al., 2008), to address spatio-temporal questions concerning treatment use (i.e., both occupancy and intensity of use) by Canada lynx. Our application of hurdle models was similar to evaluations of patch occupancy and intensity of use for woodland caribou (*Rangifer tarandus caribou*) in residual forest stands (Lesmerises et al., 2013).

2.2.2. Canada lynx data

We used a dataset of GPS locations (164,593 locations; Fig. 1) from Canada lynx that occupied managed landscapes to assess their use of silvicultural treatments. During 2004–2015, we captured and equipped 66 lynx with store-on-board GPS units (Lotek Wireless, Newmarket, Ontario, Canada or Sirtrack Ltd., Havelock North, New Zealand). Our capture efforts were approved by the Institutional Animal Care and Use Committee (University of Montana IACUC permits 4–2008 and TE053737–1). We programmed GPS collars to collect a location every 30 min for 24 h every other day for the life of the collar (generally 6–8 months). Spatial accuracy of locations averaged 30 m as reported by Squires et al. (2013) and fix rate was approximately 86% (see Holbrook et al., 2017a for additional details on GPS data processing). We assessed occupancy and intensity of use of treated patches across seasons, which we defined as summer (April – October) and winter (November – March).

2.2.3. Stratifying silvicultural treatments with the Normalized Burn Ratio

We used the U.S. Forest Service's FACTS database to identify different silvicultural treatments that occurred within Canada lynx home ranges (home ranges defined in Holbrook et al., 2017a). The FACTS database is a patch-based geospatial layer of silvicultural actions with records going back to the 1920s. Although useful for many research applications (e.g., see applications of FACTS in Zielinski et al., 2013; Tempel et al., 2014; Sweitzer et al., 2016), FACTS data suffers from spatio-temporal errors in terms of treatment extent within polygons and timing of implementation. Therefore, while others have assumed differences among treatment strata derived from FACTS, we implemented a novel assessment to validate our stratification using a time-series of the NBR.

We used the FACTS database to develop an initial set of six forest treatments, which were composed of 25 unique silvicultural activity types (Appendix A: Table A1). The six silvicultural treatments

included: (1) group selection cut ($n = 11$; trees harvested in small patches usually less than 1 ha and regenerated naturally or by planting), (2) liberation cut ($n = 60$; overstory or competing trees removed moved to liberate subject trees), (3) improvement cut ($n = 85$; removing trees from all size classes as to improve the residual tree quality and growth rates), (4) precommercial thinning ($n = 346$; thinning small trees ~15 cm as to modify species composition and provide growing space for residual trees), (5) regeneration cut with natural regeneration ($n = 360$; clearcut resulting in the remove all or the majority of high forest cover as to regenerate a stand from seed), (6) regeneration cut with planting ($n = 431$; clearcut resulting in the removal of all or the majority of high forest cover and plant trees). We expected regeneration cuts to represent the most severe impact to vegetation followed by selection cut, liberation cut, improvement cut, and precommercial thinning; a total of 1,293 treated patches (i.e. silvicultural cuts or thinnings) were included in this analysis. We only considered patches that were modified through a single action (i.e., we excluded patches with multiple treatment actions) and we discarded any patches that were affected by wildfires.

To evaluate vegetation impact and recovery we assessed how the NBR changed as a function of treatment type and time since treatment. We developed the time-series of NBR for our study area using the Landsat archive as part of the time-series analysis in Savage et al. (2018). We calculated the mean NBR across all treatment patches for each year since treatment (starting at year $t-1$). We then evaluated how mean NBR ($\pm 90\%$ CIs) for each year and treatment changed as a function of time since treatment. For this analysis, our temporal gradient ranged up to 39 years after a treatment. Our premise was that if the silvicultural treatments created distinct vegetation conditions after a harvest, the trajectory of vegetation recovery (indexed via NBR) would differ by treatment type. We used program R (R Core Team, 2017) to complete these analyses.

Our initial assessment of the NBR across time since treatment indicated there were some natural groupings among different treatment types (Fig. 2a). For instance, liberation cuts and group selection cuts, as well as improvement cuts and precommercial thinnings, generated similar NBR trajectories (Fig. 2a). Therefore, we reclassified our treatments into the following strata (Appendix A: Table A1): (1) regeneration cuts (combined regeneration cut with natural regeneration and regeneration cut with plantings; $n = 791$), (2) selection cuts (combined group selection and liberation cut; $n = 71$), and (3) thinnings (combined improvement cut and precommercial thinning; $n = 431$). We then repeated our NBR analyses with these combined strata, which demonstrated the distinct patterns of vegetation change across these three groups (Fig. 2b). Consequently, we used these three treatments as our final suite of silvicultural actions (regeneration cut, selection cut, and thinning), which captured a low (e.g., thinning) to high (e.g., regeneration cut) gradient in treatment severity.

In order to ensure that our treatment stratification was relevant to Canada lynx ecology, we calculated the range of NBR at GPS locations for all lynx ($n = 64$ lynx, 63,204 locations) sampled during the winter season. We used the winter season because winter is when lynx exhibit more specificity in habitat selection (Squires et al., 2010; Holbrook et al., 2017a). Based on previous work highlighting the disproportionate use of mature forest structures by lynx (Squires et al., 2010; Holbrook et al., 2017a), we expected lynx to use a high value and narrow range of the NBR, indicative of recovered vegetation. We calculated a mean NBR (from 2013) for each lynx and subsequently calculated the interquartile range (IQR). We then evaluated how the IQR related to the NBR trajectories associated with our three silvicultural treatments (Fig. 2b). Consistent with our hypothesis, Canada lynx used a high value and narrow range of the NBR (lynx IQR in Fig. 2b) indicating that our stratification of silvicultural treatments was relevant to lynx.

Table 3

Standardized regression coefficients for covariates within the selected hurdle models characterizing how silvicultural treatment influenced patch occupancy and intensity of use by Canada lynx (*Lynx canadensis*). Coefficients are shown for both the binomial and negative binomial regressions, characterizing occupancy and intensity of use, respectively. Bold indicates support for a spatio-temporal functional response in patch use by lynx. TST indicates time since treatment, Adv Regen indicates advanced regeneration, and Stand Init indicates stand initiation.

Covariate	Regeneration cut		Selection cut		Thinning	
	Winter	Summer	Winter	Summer	Winter	Summer
TST						
Occupancy	0.442	0.051	0.381	0.138	0.054	−0.040
Intensity of use	0.614	0.079	0.298	0.267	0.158	−0.096
Mature						
Occupancy	–	–	−0.346	–	−0.335	0.267
Intensity of use	–	–	−0.314	–	0.256	−0.161
Adv regen						
Occupancy	–	−0.093	–	0.002	−0.207	0.570
Intensity of use	–	−0.064	–	0.221	−0.029	−0.133
Stand Init						
Occupancy	–	–	–	–	−0.285	0.095
Intensity of use	–	–	–	–	0.389	0.194
TST mature						
Occupancy	–	–	−0.126	–	–	–
Intensity of use	–	–	−0.409	–	–	–
TST Adv Regen						
Occupancy	–	0.057	–	–	–	–
Intensity of use	–	0.145	–	–	–	–

† 1.5 km neighborhood.

‡ 4 km neighborhood.

* $\alpha < 0.10$.

** $\alpha < 0.05$.

*** $\alpha < 0.01$.

seasons and lynx responses (i.e., occupancy and intensity of use; Table 3). The probability of lynx occupancy during winter was negatively related to the amount of stand initiation and mature forest in the neighborhood, whereas the intensity of lynx use was positively related to these two variables (Table 3). During summer, lynx occupancy was positively related to the amount of advanced regeneration and mature forest in the neighborhood, but contrastingly the intensity of lynx use was negatively related to these factors (Table 3). The intensity of lynx use was also positively related to the amount of stand initiation in the neighborhood (Table 3). In contrast to regeneration and selection cuts, the forest structure surrounding a thinning treatment was consistently more important for lynx use than the effect of time since treatment.

All model evaluations provided evidence of appropriate model fit. The correlations between observed and expected counts > 0 were consistently high, which suggested strong model performance (Table 2; $r \geq 0.95$). In addition, we observed no consistent spatial autocorrelation in the residuals (all Moran's I values ≤ 0.10) across all lag distances.

4. Discussion

Relatively few studies have evaluated the effect of different silvicultural actions on the resource use of forest carnivores (e.g., Cushman et al., 2011; Tigner et al., 2015; Scratford et al., 2017), despite the management controversy associated with manipulating forests occupied by these sensitive species (e.g., Howard, 2014). To our knowledge, our work is the first to assess the effect of silvicultural actions on Canada lynx. Importantly, we discovered that lynx use silvicultural treatments. However, use of any treatment (i.e., regeneration cut, selection cut, or thinning) was low up to ~ 10 years post-treatment. This suggests there is a cost regardless of treatment type, which is consistent with previous work highlighting a ~ 10 year negative impact of pre-commercial thinning on snowshoe hare densities (Homyack et al., 2007). The alignment of these ~ 10 year responses for lynx and

snowshoe hares is consistent with ecological predictions because Canada lynx rely heavily on snowshoe hares as a prey resource (e.g., Mowat et al., 1996; Squires and Ruggiero, 2007; Ivan and Shenk, 2016). In addition, we found that Canada lynx use thinning treatments at a faster rate over time than either selection or regeneration harvests (Fig. 4). Contrary to our expectations, lynx used selection and regeneration cuts similarly over time despite the differences we observed in vegetation impact as measured via NBR (Fig. 2). Moreover, the composition and abundance of forest structural stages surrounding a particular treatment (e.g., Fig. 3) influences how lynx use that treatment. In some cases, both the probability of occupancy and the intensity of patch use by Canada lynx was influenced by the surrounding forest structure, which exemplified a spatial functional response in habitat use (*sensu* Mysterud and Ims, 1996). This was similar to previous work demonstrating the importance of the surrounding landscape for the patch use of woodland caribou (Lesmerises et al., 2013) and pygmy rabbits (*Brachylagus idahoensis*; McMahon et al., 2017). However, patch use by Canada lynx was also characterized by an interaction between time since treatment and the composition of forest structure in the neighborhood, which indicated a spatio-temporal functional response (Fig. 5). In other words, vegetation recovery after a silvicultural treatment and the existing forest structure surrounding a treatment interactively influenced the behavior of Canada lynx. Collectively, this work fills an important knowledge gap in Canada lynx spatial ecology. Forest managers can apply our spatio-temporal understandings to develop refined strategies aimed at both forest management and lynx habitat conservation.

The relationship between time since treatment and patch use by Canada lynx was generally similar across our univariate and regression analyses. For instance, our univariate assessments indicated lynx use thinnings sooner after a harvest than selection or regeneration cuts (Fig. 4), which aligned with our index of treatment severity based on the NBR (Fig. 2). Our regression analyses indicated that the effect of time since treatment was always positive for lynx use, but the effect was

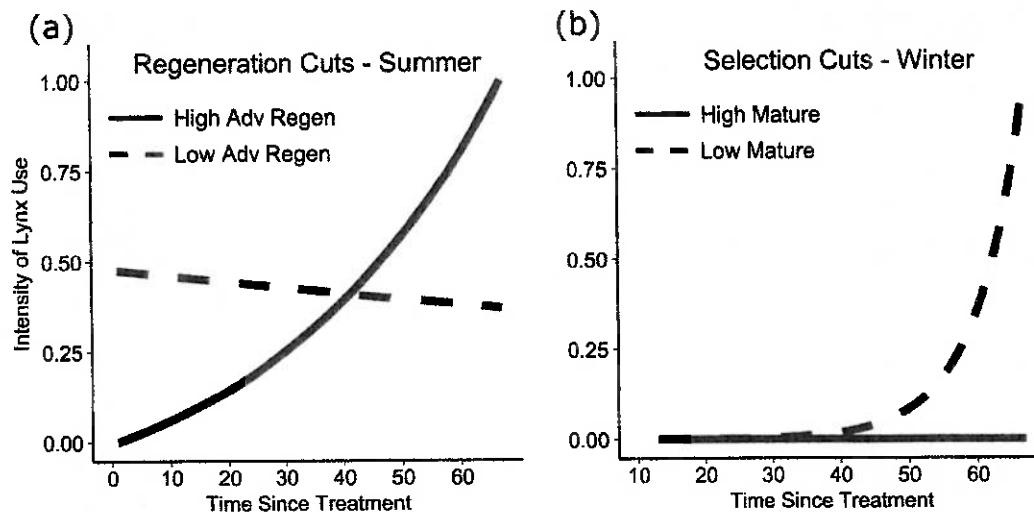


Fig. 5. Spatio-temporal interactions (i.e., a spatio-temporal functional response) predicted from our selected hurdle models characterizing the intensity of Canada lynx (*Lynx canadensis*) use (scaled between 0 and 1) for regeneration and selection cuts. In other words, the intensity of lynx use within a patch depends on the amount of advanced regeneration or mature forest in the 4 km and 1.5 km neighborhood (respectively) surrounding the patch as well as the time since treatment. Predicted intensity of use was generated from the negative binomial regression within the hurdle model. (a) Indicates the predicted intensity of lynx use during summer for patches that received a regeneration cut. (b) Indicates predicted intensity of lynx use during winter for patches that received a selection cut. The proportion for 'High Adv Regen' was 0.30 and 'Low Adv Regen' was 0.10, while the proportion for 'High Mature' was 0.80 and 'Low Mature' was 0.30. Adv Regen indicates advanced regeneration.

stronger for regeneration cuts followed by selection cuts and thinnings, respectively (Tables 2 and 3; again, aligning with treatment severity). Finally, as predicted, time since harvest generally exhibited a stronger effect on lynx use during the winter as compared to the summer (Table 3), but this was only apparent in our regression analyses.

These temporal patterns were consistent with habitat selection by Canada lynx in the Rocky Mountains, U.S. For example, Canada lynx exhibit strong multi-scale selection for advanced regeneration and mature forest likely because of abundant and accessible snowshoe hares (Squires et al., 2010; Ivan et al., 2014; Ivan and Shenk, 2016; Holbrook et al., 2017b). In our study area, the stage of advanced regeneration takes at least ~25 years to develop (Holbrook et al., 2017a), which aligns with the initial use of regeneration and selection cuts by lynx (Fig. 4a and 4c). Further, Canada lynx increasingly use mature structural stages during the winter months (Squires et al., 2010; Holbrook et al., 2017a), suggesting more time might be needed to develop winter habitat as compared to summer habitat. Heterogeneous disturbances such as thinnings, however, seemingly facilitate the development of advanced regeneration and mature forests at a faster rate than selection or regeneration harvests given the earlier use by lynx (Fig. 4c). These results have implications concerning the temporal dimensions of forest treatments aimed at improving Canada lynx habitat.

Furthermore, lynx exhibited different responses to the composition of forest structural stages in the neighborhood surrounding thinnings based on the hierarchical level of behavior; that is, the probability of lynx occupancy (first level) and the intensity of lynx use (second level). Many studies have demonstrated the hierarchical habitat relationships (e.g., Johnson, 1980; Kettle and Messier, 2000; DeCesare et al., 2012; Holbrook et al., 2017a; McMahon et al., 2017), and our insights build on this work. For instance, increasing stand initiation in the neighborhood negatively influenced lynx occupancy of thinnings during the winter. This is likely because Canada lynx strongly avoid stand initiation (Holbrook et al., 2017a), and particularly so in the winter, thus decreasing the probability of patch use when stand initiation is abundant in the surrounding area. In contrast, stand initiation positively influenced the intensity of lynx use within a thinned patch during the winter and summer. This was conceivable because once a lynx occupies a thinning, they might then chose to remain within the patch versus

moving out into an avoided structural stage (i.e., stand initiation). Other studies using analytical procedures similar to ours have demonstrated differential responses depending on the hierarchical level of the response (e.g., occupancy or intensity of use) for woodland caribou and pygmy rabbits (Lesmerises et al., 2013; McMahon et al., 2017).

We also observed situations where the effect of forest structure in the surrounding neighborhood was similar across the hierarchical levels of behavior. For example, Canada lynx exhibited a reduced probability of occupancy and intensity of use for treated patches when the neighborhood contained abundant mature forest (Table 3). In fact, when mature forest was abundant in the neighborhood of selection cuts, the intensity of use by Canada lynx remained low regardless of time since treatment (Fig. 5b). The negative influence of mature forest on lynx resource use was likely associated with the benefits provided by mature forests resulting in lynx selecting this stage and avoiding the treated patches nearby. A similar mechanism was suggested to explain the fast and direct movement of Pacific marten through resource-poor stands (i.e., open areas) versus the slow, more deliberate movements in resource-rich stands (Moriarty et al., 2016). Mature forests provide abundant, temporally stable, and accessible snowshoe hares within the Rocky Mountains (Griffin and Milk, 2009; Ivan et al., 2014; Ivan and Shenk, 2016; Holbrook et al., 2017b), and therefore lynx spend a substantial amount of time within this structural stage (Squires et al., 2010; Holbrook et al., 2017a).

Our suite of insights concerning the spatio-temporal responses of Canada lynx to silvicultural actions were in part a result of our novel approach to stratifying silvicultural treatments. We retroactively evaluated vegetation responses over time using the NBR, which ensured our treatment stratification was ecologically relevant. We then demonstrated that this approach related to Canada lynx, with lynx using a high value and narrow range of NBR (Fig. 2). Future work examining animal responses to forest manipulations could apply our approach to characterize ecologically distinct treatments through time. This is an important contribution because often it is assumed that different database labels, such as classifications of silvicultural actions (e.g., with the FACTS database), represent ecological differences, which we demonstrated to be a false assumption (e.g., Fig. 2a).

5. Conclusion

A difficult challenge within publically managed forests lies at the intersection of silvicultural actions and the management of forest-dwelling species that are of conservation concern (e.g., Stephens et al., 2014; Howard, 2016). To assist in narrowing the gap between silviculture and species conservation, we evaluated how forest treatments influence resource use of Canada lynx, a threatened carnivore in the contiguous U.S. (USFWS, 2000). First, we demonstrated that lynx clearly use silviculture treatments, but there is a ~10 year cost of implementing any treatment (thinning, selection cut, or regeneration cut) in terms of resource use by Canada lynx. This temporal cost is associated with lynx preferring advanced regenerating and mature structural stages (Squires et al., 2010; Holbrook et al., 2017a) and is consistent with previous work demonstrating a negative effect of precommercial thinning on snowshoe hare densities for ~10 years (Homyack et al., 2007). Second, if a treatment is implemented, Canada lynx used thinnings at a faster rate post-treatment (e.g., ~20 years post-treatment to reach 50% lynx use) than either selection or regeneration cuts (e.g., ~34–40 years post-treatment to reach 50% lynx use). Lynx appear to use regeneration and selection cuts similarly over time suggesting the difference in vegetation impact between these treatments made little difference concerning the potential impacts to lynx (Fig. 4c). Third, Canada lynx tend to avoid silvicultural treatments when a preferred structural stage (e.g., mature, multi-storied forest or advanced regeneration) is abundant in the surrounding landscape, which

highlights the importance of considering landscape-level composition as well as recovery time. For instance, in an area with low amounts of mature forest in the neighborhood, lynx use of recovering silvicultural treatments would be higher versus treatments surrounded by an abundance of mature forest (e.g., Fig. 3b). This scenario captures the importance of post-treatment recovery for Canada lynx when the landscape context is generally composed of lower quality habitat. Overall, these three items emphasize that both the spatial arrangement and composition as well as recovery time are central to balancing silvicultural actions and Canada lynx conservation. Our work here represents an important step in filling knowledge gaps at the intersection of disciplines, such as silviculture and animal ecology, which is essential for the future development of pragmatic solutions.

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Appendix A.

Silvicultural treatment stratification from the U.S. Forest Service's FACTS database.

Table A.1

Reclassification table showing the raw classification from the U.S. Forest Service's FACTS database to our first and final set of silvicultural treatments.

FACTS labels	First set of potential treatments	Final set of treatments
Group selection cut	Group selection cut	Selection cut
Single-tree selection cut	Group selection cut	Selection cut
Liberation cut	Liberation cut	Selection cut
Shelterwood preparatory cut	Improvement cut	Thinning
Improvement cut	Improvement cut	Thinning
Seed-tree preparatory cut	Improvement cut	Thinning
Commercial thin	Improvement cut	Thinning
Stand clearcut	Regen cut	Regen cut
Patch clearcut (w/leave trees)	Regen cut	Regen cut
Stand clearcut (w/leave trees)	Regen cut	Regen cut
Patch clearcut	Regen cut	Regen cut
Seed-tree final cut	Regen cut	Regen cut
Seed-tree seed cut (with and without leave trees)	Regen cut	Regen cut
Shelterwood establishment cut (with or without leave trees)	Regen cut	Regen cut
Two-aged seed-tree seed and removal Cut (w/res)	Regen cut	Regen cut
Two-aged shelterwood establishment and removal Cut (w/ res)	Regen cut	Regen cut
Two-aged shelterwood establishment Cut (w/res)	Regen cut	Regen cut
Certification of natural regeneration with site prep	Natural regen	NA
Certification of natural regeneration without site prep	Natural regen	NA
Initiate natural regeneration	Natural regen	NA
Fill-in or Replant Trees	Planted	NA
Plant Trees	Planted	NA
Planting propagules and cuttings	Planted	NA
Wildlife habitat seeding and planting	Planted	NA
Precommercial thin	Precommercial thin	Thinning



Management of forests and forest carnivores: Relating landscape mosaics to habitat quality of Canada lynx at their range periphery

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ABSTRACT

Connecting forest management with the conservation of forest-associated animals requires an understanding of habitat quality, as well as identifying long-term silvicultural strategies that align with high quality habitat. It is, therefore, essential to characterize the spatio-temporal dimensions of habitat quality. Here, we leveraged multiple datasets to assess high quality habitat for female Canada lynx (*Lynx canadensis*), a federally threatened forest carnivore in the contiguous U.S. Our datasets included a spatially extensive sample of snowshoe hares (*Lepus americanus*) collected in 2013 ($n = 1340$ plots), an expansive time-series (i.e., 1972–2013) of forest structural classes derived from remote sensing, and a longitudinal dataset where we monitored habitat use and the reproductive success (i.e., litter of kittens present or absent) of female Canada lynx during 1999–2013 ($n = 32$ female lynx over 92 lynx years). Our results indicated that the probability of a female producing kittens was most associated with the connectivity of mature, multistoried forests (composed of mostly spruce-fir). However, the variation among female lynx accounted for $\approx 62\%$ of the total variation explained in litter production, suggesting substantial individual-level variation. Thus, managers can contribute to increased reproductive success of female Canada lynx by facilitating the development of mature forests, but measuring that success will be difficult given the individual variation. In core areas of high quality females (i.e., produced kittens frequently), mature forest was 17% more abundant (i.e., $\approx 60\%$ of the total core area), more connected, less clumpy, and exhibited 2.25-times larger patch sizes than the core areas of low quality females. At the home-range extent, patterns were less pronounced while the abundance of mature forests remained high ($\approx 50\%$) for high quality females. Additionally, we demonstrated that the relative density of snowshoe hares was ≈ 2.8 times higher in advanced regenerating forests compared to all other structural classes, including mature forest. Advanced regenerating forests accounted for ≈ 18 –19% of the core area and home range of high quality female lynx. Combined, our results suggest that a high quality mosaic for female Canada lynx contains ≈ 50 –60% mature forest and ≈ 18 –19% advanced regenerating forest. Furthermore, we used Forest Inventory and Analysis data to characterize the approximate age distribution of advanced regeneration and mature forest, which was relevant for rotation schedules of forest silviculture. Results indicated that advanced regeneration was ≈ 20 to 80 years old while mature forest was ≈ 50 to ≥ 200 years old. Our results provide novel insight into how forest management could increase habitat quality for female Canada lynx, and suggest that multiple silvicultural methods (e.g., intermediate treatments, regeneration harvests) could be employed to maintain a forest mosaic that enhances the ability of females to produce kittens. We concluded by providing a framework that integrates our new insights into a management context with the aim of conserving Canada lynx on multiple-use lands.

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NR = 18-66
Med = 44 35-16,256
23km² 417 5620
424
418
med = 23km² =
5667

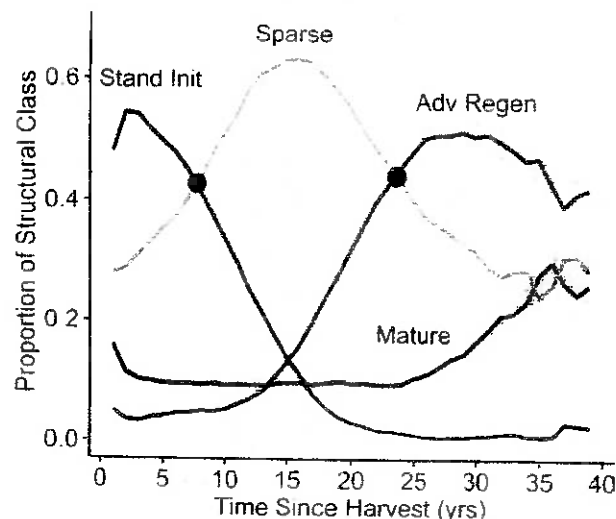


Fig. 4. Temporal transitions of forest structural classes in the context of a vegetation reset from a regeneration cut (e.g., a clearcut, $n = 791$) during 1973–2013 (i.e., 1–39 years post-harvest). Lines indicate mean proportions ($\pm 90\%$ CIs) and black dots indicate dominance transition points. The stand initiation class dominated during ≈ 1 –8 years post-harvest, followed by sparse and advanced regeneration. We did not observe the full time sequence required to develop elements of mature forest given our time series, indicating this class takes at least ≈ 50 years to begin establishing after a reset.

indicative of the many different forms of sparse forest (e.g., could be young or old). The advanced regeneration class was low for the first ≈ 15 years after harvest, after which it increased and dominated from ≈ 25 years post-harvest throughout the remaining portion of our time frame (i.e., 39 years; Fig. 4). We did not observe the time frame in which the mature structural class began to dominate, indicating that it takes at least ≈ 50 years or more for elements of a mature forest to develop (Fig. 4). This temporal context of successional changes associated with silviculture provides managers with the information necessary to develop harvest rotations.

3.3. Forest mosaics, core use areas, and female quality of Canada lynx

We monitored 32 females over the course of 92 potential reproductive events. Of those, we observed 62 litters of kittens, which resulted in an overall kitten production rate of 67%. The median home range size for females was 23 km^2 (range = 18 – 66 km^2), while the median core use area was 6 km^2 (range = 3 – 21 km^2).

The proclivity of female lynx to produce kittens was influenced by the amount and arrangement of forest structural classes in home ranges, especially in core use areas. Our results supported (i.e., $\Delta\text{AIC}_c \leq 2$) multiple models, but the top model (i.e., $\Delta\text{AIC}_c = 0$) suggested lynx were most influenced by the mature forest connectivity index (MFCI) and the percentage of the landscape that was stand initiation (Table 1). The regression coefficients (i.e., unstandardized) indicated that the effect of both explanatory variables were significant: $\beta_{\text{MFCI}} = 3.33$ (90% CI = 0.84 – 6.52) and $\beta_{\text{StandInit}} = 0.18$ (90% CI = 0.02 – 0.37). The effect of advanced regeneration was also included within the supported model set (Table 1), but the relationship was not statistically significant: $\beta_{\text{AdvRegen}} = 5.06$ (90% CI = -2.00 to 13.01). The marginal and conditional coefficient of determination from our top model was $R_m^2 = 0.15$ and $R_c^2 = 0.39$, respectively, which indicated substantial individual variation among female lynx in their ability to produce litters of kittens. Indeed, approximately 62% of the total variation explained (i.e., $(0.39 - 0.15) / 0.39 = 62\%$) was attributed to among individual variation. Furthermore, the null model that only incorporated the random effect of female lynx was within our supported set, once again suggesting considerable individual variation. Nevertheless, the marginal

Table 1

Models assessing the influence of forest structure and arrangement on the proclivity of female Canada lynx (*Lynx canadensis*) to produce litters of kittens. For each model, we provided the log-likelihood (LL), ΔAIC_c , and AIC_c weights (w). As a measure of fit, we calculated a generalized measure of R^2 from our top (i.e., $\Delta\text{AIC}_c = 0$) generalized linear mixed-model (Nakagawa and Schielzeth 2013). Our marginal (fixed factor variation) and conditional (total variation) estimates were $R_m^2 = 0.15$ and $R_c^2 = 0.39$, respectively. Abbreviation MFCI indicates the mature forest connectivity index. Metrics characterizing the proportion of the landscape (PLAND) and the clumpiness index (CLUMPY) were abbreviated.

Model Description	LL	ΔAIC_c	w
MFCI + PLAND Stand Initiation	-51.60	0.00	0.27
MFCI	-53.27	1.09	0.16
Null	-54.63	1.67	0.12
MFCI + CLUMPY Adv Regeneration	-52.56	1.86	0.11
MFCI + CLUMPY Adv Regeneration + PLAND Stand Initiation	-51.55	2.09	0.10
MFCI + PLAND Stand Initiation + PLAND Sparse	-51.60	2.19	0.09
MFCI + PLAND Sparse	-53.22	3.17	0.06
MFCI + CLUMPY Adv Regeneration + PLAND Sparse	-52.14	3.26	0.05
MFCI + CLUMPY Adv Regeneration + PLAND Stand Initiation + PLAND Sparse	-51.44	4.14	0.04

^a At the core use area.

^b At the home range.

effects of MFCI and the percent stand initiation were significant and accounted for the remaining 38% of the total variation explained.

Because it was inappropriate to model average regression coefficients derived from generalized linear models (Cade 2015), we performed our sensitivity analysis with only our top model. This analysis provided a more resolved understanding concerning the relationship between forest structure and the probability of a female lynx producing a litter of kittens. Despite the statistical effect of both MFCI and percent stand initiation from our GLMM, our sensitivity analysis indicated that litter production was substantially more sensitive to changes in MFCI than the percent stand initiation per se (Fig. 5). For instance, the R^2 between MFCI and the probability of producing a litter was 0.30, while the R^2 associated with stand initiation was 0. However, it is important to note that as stand initiation increases within a core use area, mature forest will (at some point) by definition decrease resulting in a reduction of the MFCI. Although more sensitive to MFCI, our analysis further indicated that the probability of producing a litter varied substantially among female lynx (e.g., see spread in Fig. 5).

To assign our index of quality to each female lynx, we averaged the predicted probabilities of producing a litter across our model set, which is an appropriate technique to incorporate prediction uncertainty (rather than averaging model coefficients and subsequently generating predictions; Cade 2015). The averaged predicted probabilities of producing a litter of kittens ranged from 0.30 to 0.92 across the 32 females. This resulted in the following categorization of females into low, medium, and high quality: low quality probabilities = 0.30 – 0.51 ($n = 10$ females), medium quality probabilities = 0.60 – 0.80 ($n = 11$ females), and high quality probabilities = 0.81 – 0.92 ($n = 11$ females).

The number and arrangement of core use units within core areas was generally similar across the gradient in female quality (Table 2, Fig. 6). Females exhibited ≈ 2 – 5 spatially separate units within core use areas irrespective of the ability for females to produce kittens. Further, the average nearest neighbor distance between core use units was similar ($\approx 1600 \text{ m}$) between low and medium quality female lynx (Table 2). However, there was evidence suggestive of high quality females having more spatially centralized core areas based on their lower nearest neighbor distance among core use units ($\approx 1100 \text{ m}$; Table 2) when compared to medium quality females, providing some support for our predictions.

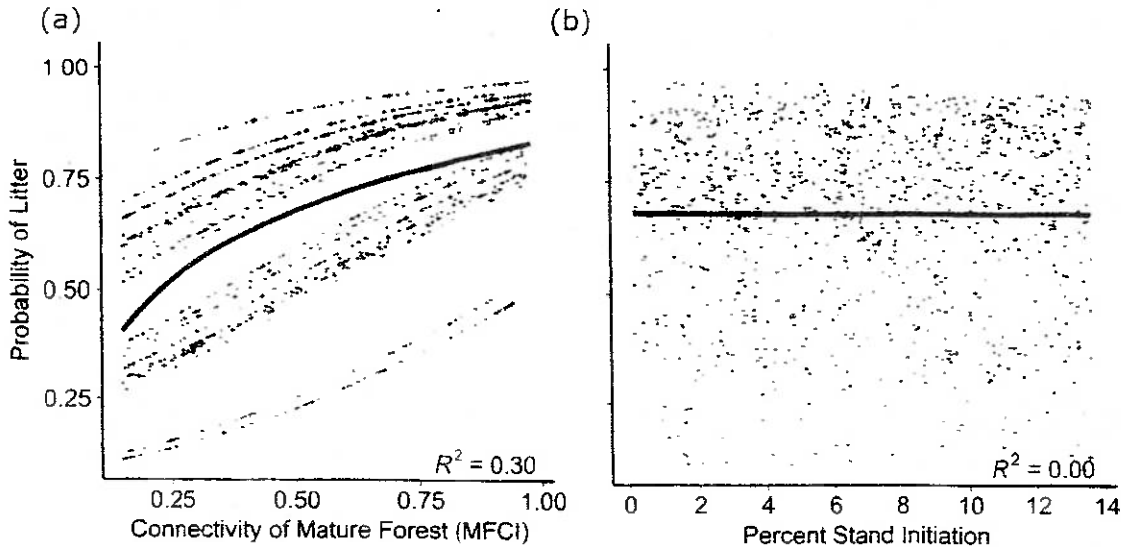


Fig. 5. Sensitivity of litter production by female Canada lynx (*Lynx canadensis*) to changes in forest structure. Each data point represents one realization of 1000 randomizations of mature forest connectivity (at the core use scale), percent stand initiation (at the core use scale), and the identity of female lynx: (a) indicates a log-linear relationship between the variation in mature forest connectivity index (MFCI) and the probability of producing a litter, (b) indicates no relationship between the variation in percent stand initiation and the probability of producing a litter.

Table 2

Median (M) and interquartile range (IQR) of the number of core use units and average nearest neighbor distance among core use units within core areas across our gradient of female quality for Canada lynx (*Lynx canadensis*). Female quality was based on their probability of producing a litter of kittens: low quality = probability of litter 0.30–0.51 ($n = 10$), medium quality = probability of litter 0.60–0.80 ($n = 11$), and high quality = probability of litter 0.81–0.92 ($n = 11$).

Female Quality	Characteristics of Core Use Areas	
	Number of spatial units	Distance between spatial units (m)
Low	M: 2.5	M: 1571
	IQR: 2–4	IQR: 435–2670
Med	M: 3	M: 1705
	IQR: 1.5–6	IQR: 280–2464
High	M: 3	M: 1108
	IQR: 2–4.5	IQR: 640–1682

To summarize differences in forest structure and arrangement across categories of female quality, we focused on comparisons between low and high quality females (Table 3, Fig. 7, Appendix B). Of these comparisons, we found that forest structure in core use areas distinguished female quality more than the overall home range. For instance, we observed differences across classes of female quality within core use areas 70% of the time, versus 30% and 50% of the time at non-core use areas and home ranges, respectively (Table 3, Appendix B). Thus, the abundance and arrangement of structural classes in core use areas had the greatest influence on reproductive success for female Canada lynx.

Low quality and high quality female Canada lynx exhibited differences in many metrics of forest structure. Mature forest was 17% more abundant (median = 58%, IQR = 55–65%) and was more connected, less clumpy, and exhibited 2.25-times larger patch sizes in core use areas of high quality females compared to low quality females (Table 3, Figs. 7, 8, Appendix B). Indeed, mature forest was 2.5-times more abundant than any other structural class in the core use areas of high quality females (Table 3). The abundance, patch size, and connectance of mature forest were all higher at the core use area than at the non-core area (Table 3, Figs. 7, 8). These differences indicated the distinctiveness of core use areas and the importance of mature forest as the landscape matrix.

We discovered differences between low and high quality females for the remaining forest structural classes as well. High quality females exhibited 3% more stand initiation (median = 4%, IQR = 2–6%) and 8% less advanced regeneration (median = 18%, IQR = 12–24%) along with 14% less sparse forest (median = 23%, IQR = 17–24%) than did low quality females (Table 3). Further, high quality females displayed smaller patches of advanced regeneration and larger patches of sparse forest when compared to low quality females (Figs. 7, 8, Appendix B). The clumpiness and connectance of sparse forest were both lower for high quality females than low quality females. However, patches of advanced regeneration were clumpier and more connected for high quality females (Figs. 7, 8, Appendix B). Lastly, patches of sparse forest were more irregularly shaped in core areas of low quality females relative to high quality females. We observed no differences in the remaining comparisons within core use areas of female lynx.

4. Discussion

Our objective was to inform the intersection of forest management and Canada lynx conservation by providing detailed information characterizing high quality habitat. We confirmed (similar to Kosterman et al., 2018) that core use areas (3–21 km²), which can be one spatial unit or many (Figs. 6, 8), are more important than aspects of the entire home range (18–66 km²) for litter production by female Canada lynx. This does not, however, mean that home ranges of female lynx are unimportant, and indeed home ranges are by definition a defended area that females have chosen to occupy. Further, all categories of female quality exhibited a similar number of spatial units within core use areas, and there was only moderate support for units closer together within high quality females. We discovered that the productivity of females was most sensitive to the connectivity of mature, multistoried forests (composed of mostly spruce-fir) within core use areas, but litter production also varied substantially among females (i.e., 62% of the variation explained) for reasons we did not measure. Mature forest was more abundant, connected, and exhibited 2.25-times larger patch sizes in core areas of high quality females versus low quality females. The positive relationship between litter production and the connectivity of mature forest was likely a result of mature forest providing temporally consistent and accessible snowshoe hares as prey (e.g., Griffin and Mills, 2009; Squires et al., 2010; Ivan et al., 2014; Ivan and Shenk,

1155 m²
8.00
3-21
km²
734 ac
5178 ac

reproduction and our conclusions assume high female survival. We reinforced the findings of Kosterman et al. (2018) that core use areas within a home range context (see Figs. 6, 8) are a unique and important component for successful reproduction, although substantial residual variation exists among female lynx. Further, we demonstrated that (1) the probability of producing kittens by female lynx was most sensitive to the connectivity of mature, multistoried forests (composed of mostly spruce-fir), (2) the relative density of snowshoe hares was ≥ 2.8 times higher in advanced regenerating stands relative to other forest structures, including mature forest, (3) the home range ($\approx 18\text{--}66\text{ km}^2$) and core use area of high quality females was composed of $\approx 50\text{--}60\%$ mature forest and $\approx 18\text{--}19\%$ advanced regeneration, and (4) advanced regenerating and mature forests were $\approx 20\text{--}80$ years old and ≈ 50 to ≥ 200 years old, respectively, highlighting the developed nature of high quality Canada lynx habitat. This essential information, coupled with how lynx respond to silvicultural treatments (Holbrook et al., 2018), allows forest managers to develop and apply strategies that incorporate forest management and lynx conservation over the long term within a multiple-use context (e.g., Fig. 9).

However, one of the most difficult challenges currently facing forest management in the western U.S. is increasing wildfire seasons and activity (e.g., Westerling et al., 2006; Abatzoglou and Williams, 2016; Westerling, 2016). Increasing wildfire also complicates the conservation of high quality Canada lynx habitat because quality habitat contains older forest structures and, thus, relatively high fuel loads. Therefore, an important step forward for Canada lynx conservation will be evaluating forest management alternatives that are capable of balancing wildfire risk and the conservation of lynx habitat. Indeed, continuing to assess knowledge gaps at the intersection of forest management, natural and anthropogenic disturbance, and species conservation will be essential for future conservation efforts on western forests.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.01.011>.

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Sciurid Habitat Relationships in Forests Managed Under Selection and Shelterwood Silviculture in Ontario

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Abstract

Although partial forest harvesting is practiced over large areas, managers know little about its impacts on sciurid rodents, particularly on northern (Glaucomys sabrinus) and southern flying squirrels (G. volans) in the northeastern United States and Canada. We examined habitat relationships of sciurid rodents (northern flying squirrels, southern flying squirrels, red squirrels [Tamiasciurus hudsonicus], and eastern chipmunks [Tamias striatus]) at 2 spatial scales in managed and unmanaged coniferous and hardwood forests of Algonquin Provincial Park, Ontario, Canada. We live-trapped rodents in 26 northern hardwood stands and in 16 white pine (Pinus strobus) stands from 2002 to 2004. Northern flying squirrel and red squirrel densities were significantly lower in recently harvested (3–10 yr since harvest) shelterwood stands than in unmanaged stands. In contrast, southern flying squirrel densities were higher in selection-harvested stands than in old-forest areas. The densities of northern flying squirrels and red squirrels had a strong relationship with the density of large spruce (Picea sp.) and hardwood trees and snags in conifer sites. Southern flying squirrel numbers had a positive association with the density of mast trees at the landscape level but not at the stand level in hardwood forests. Eastern chipmunk density had a positive correlation with the volume of old downed woody debris and the stems per hectare of declining trees. We recommend forest managers retain more large spruce and hardwood trees to mitigate the impacts of shelterwood harvesting on northern flying squirrels and red squirrels, and that they maintain high mast availability at the landscape level to ensure the persistence of southern flying squirrels. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1735–1745; 2006)

Key words

eastern chipmunk, Glaucomys sabrinus, Glaucomys volans, habitat use, northern flying squirrel, Ontario, partial harvesting, red squirrel, southern flying squirrel, stepwise regression, Tamias striatus, Tamiasciurus hudsonicus.

Many jurisdictions in North America, including Ontario, Canada, have selected flying squirrels (*Glaucomys* spp.) as indicators of sustainable forest management practices. This designation has resulted in a relatively large body of research on these and other tree squirrels in landscapes managed under clearcut logging (Rosenberg and Anthony 1992, Witt 1992, Carey 1995, 2000, Martin and Anthony 1999, Cote and Ferron 2001). However, partial harvesting techniques, such as selection and shelterwood logging, have received less attention. These are common silvicultural techniques employed in temperate mixedwood forests in northeastern Northern America. In these systems, forest operators remove a portion of the overstory at relatively shorter intervals (approx. 20 yr), creating a more frequent, but less intensive disturbance regime, than under clearcut logging. The effects of partial harvesting on canopy-dwelling organisms are likely to differ from those resulting from clearcutting because partial harvesting maintains a relatively closed-canopy mature forest throughout the harvest cycle. Unfortunately, only 2 studies have examined the effects of partial harvesting (shelterwood harvesting) on flying squirrels (Waters and Zabel 1995, Taulman et al. 1998). These studies found that relatively high harvest intensities (<10 m²/ha residual basal area) negatively affected flying squirrel populations. Researchers have not examined the effects of

selection harvesting systems in hardwood forests, which typically leave greater residual basal areas than shelterwood logging.

Although partial harvesting systems retain canopy cover on sites, impacts on tree squirrel populations may manifest through other logging-induced changes in forest structure. Partial harvesting typically involves a reduction in the abundance of diseased and dead trees (McComb and Lindenmayer 1999, McGee et al. 1999, Costello et al. 2000) and often results in more homogenous forest structure, with reduced tree density and size (Costello et al. 2000). These changes may be important for arboreal mammals (Gerrow 1996, Carey 2000) and could result in negative effects for cavity nesters (Imbeau et al. 2001).

Most past studies on sciurids have only considered local (site-level) effects; however, organisms may demonstrate different responses to the same factor at different scales (Wiens 1989). Studies in fragmented landscapes suggest that flying squirrels may be sensitive to area effects (Nupp and Swihart 2000) and indicate that large clearcuts may act as barriers to dispersal and movement (Bendel and Gates 1987). Taulman (1999) found that flying squirrels nested in adjacent unharvested forest following partial harvesting, suggesting that the amount and configuration of unharvested stands might modulate flying squirrel responses to forest harvesting. In concert, these studies raise the possibility that local responses to forest harvesting might,

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Table 3. Mean ($\pm$ SE) values for site-level habitat variables that differed among logged and old hardwood and pine forest sites in Algonquin Provincial Park, Ontario, Canada, 2002–2004. Variable units are the number of stems per hectare unless otherwise stated.

Habitat variable ^c	Recent cut $n = 8$, 7 ^a		Old cut $n = 8$ ^b		Old forest $n = 10$, 9 ^a		P
	Mean	SE	Mean	SE	Mean	SE	
Hardwood							
BA (m ² /ha)	19.0	1.2	20.7	0.8	31.0	1.4	<0.001
Conifer	13.1	7.7	11.5	5.9	39.9	8.4	0.020
Con ≥ 25	8.1	5.4	5.0	2.5	23.6	5.8	0.028
Hwd ≥ 25	54.5	3.8	62.4	5.0	70.4	4.0	0.044
Spruce ≥ 25	0.5	0.4	0.5	0.3	3.5	1.1	0.014
Snags	10.8	3.7	13.3	3.5	28.8	4.6	0.008
Snags ≥ 25	3.0	0.7	6.0	1.4	10.1	1.1	<0.001
Pine							
BA (m ² /ha)	20.0	1.8	NA	NA	30.7	1.3	<0.001
CanClos (%)	76.2	3.2	NA	NA	89.4	1.6	0.001
Conifer	153.8	21.5	NA	NA	229.3	25.4	0.047
Hwd ≥ 25	12.4	3.9	NA	NA	27.4	3.9	0.018
Spruce ≥ 25	3.2	1.0	NA	NA	8.1	2.1	0.080
Snags ≥ 25	4.7	1.1	NA	NA	11.1	2.0	0.022

^a Sample sizes for hardwood and pine forests, respectively.

^b We sampled old cut stands only in hardwood forests.

^c See text for definition of habitat variables.

4.7 / 11.1 = 42% loss
= 58% loss

logging histories evenly between years, and hence allow equal application of any biases among comparisons.

Habitat variable reduction and variance partitioning.—The various sciurid species tended to be more or less abundant in one forest type (hardwood or conifer), but uncommon in the other; hence, we undertook community analyses separately for hardwood and white pine sites. Because squirrel densities differed between trap years (see Table 1), we first partialled it out of the models. To examine species–habitat relationships, we performed partial redundancy analysis (RDA), which served to reduce the number of site-level habitat variables (some of which were highly correlated with each other). Initially, we entered the 17 site habitat variables into the RDA (see Habitat Measurements, above). We computed the statistical significance of each variable using Monte Carlo simulations and a forward selection routine (9,999 permutations). We sequentially removed variables that contributed little (highest non-significant P -value) until the inflation factor was <10 (ter Braak and Smilauer 1998). We retained 11 variables in the hardwood model and 9 in the white pine model.

We investigated the relative importance of site and landscape variables using variance partitioning (Borcard et al. 1992, Cushman and McGarigal 2004). This analysis measures the variation in a community matrix, explained independently and jointly by different sets of explanatory variables. We calculated the unique variation at each level (site and landscape) by partialling out (as a covariate) variation due to the other level. We performed all multi-variate analyses with CANOCO 4.5 for Windows (ter Braak and Smilauer 1998).

Individual species responses.—We plotted the density of each squirrel species against all habitat variables to ensure that assumptions of normality and homogeneity were satisfied and to check for the possibility of curvilinear relationships. We ln-transformed southern flying squirrel

densities in hardwood sites and red squirrel densities in pine sites to normalize the variance. We performed analysis of variance (ANOVA) with Bonferroni-corrected post hoc tests for each species to compare densities among years. Where a significant year effect existed ($P \leq 0.050$), we included it in all the following regression and ANOVA analyses. We analyzed the influence of logging history on squirrel density and habitat variables with ANOVA.

We used linear regression to develop sciurid habitat relationship, except in 2 instances (northern flying squirrels and red squirrels in hardwood sites) where densities were low and we therefore used logistic regression (on presence/absence). For all species, if a year effect was significant, we included it in all models. To develop site-level habitat models, we used 2 methods, stepwise regression and a priori selection of candidate variables followed by use of Akaike's Information Criterion (AIC; Burnham and Anderson 1998) to compare among models created from these candidate variables. In the former method, we used the site-level habitat variables remaining after the RDA forward selection routine. In the latter method, we picked 5–6 variables for each species that we reasoned to be most important based on relationships observed or hypothesized in the literature (listed in Table 1). From these candidate variables, we constructed all possible models of up to 3 terms and used AIC_c to compare among them. Specifically, we calculated the difference between the i th model and the minimum AIC_c (i.e., ΔAIC_c) and the Akaike weight (w_i) for each model.

To incorporate landscape-level variables into these analyses, we first forced the best site-level model into the analysis and then evaluated the value of the landscape variables in explaining additional variation in squirrel densities. We followed this hierarchical procedure for 2 reasons: 1) site-level variables proved to be more important than landscape-level variables in explaining squirrel captures

(see Results, below; see also Cushman and McGarigal 2004), and 2) in a forested landscape, we reasoned that a first-order model would incorporate local site features, whereas any landscape-level effects would be additive to these local effects. As before, we undertook both stepwise and AIC-based approaches. If results of the site-level AIC evaluation were equivocal—that is, ≥ 2 models were of approximately equal explanatory value—then we evaluated all combinations of these site models and landscape variables. For example, if 2 site-level models were equivalent, then in combination with 3 landscape variables, we evaluated 8 models (the 2 best site-level models plus 6 combinations of 1 site model plus 1 landscape variable). We performed all analyses with SPSS 11.0 (SPSS Inc., Chicago, Illinois).

Results

Over 3 summers we captured 274 individual southern flying squirrels, 83 northern flying squirrels, 1,709 eastern chipmunks, and 110 red squirrels during 28,548 trap-nights (21,091 grid-station nights). In general, small mammal populations were intermediate in abundance in 2002, high in 2003, and low in 2004. In hardwood sites, southern flying squirrel density was significantly lower in 2002 compared with 2003 (ANOVA $P=0.044$; mean MNKA/ha [$\pm$ SE] = 0.35 [0.15]), and 1.12 [0.20] for 2002 and 2003, respectively). We only analyzed grids sampled in 2002 and 2003 for southern flying squirrels because, remarkably, we did not capture a single individual in 2004. This dramatic crash in numbers appeared to be a widespread phenomenon across the far northern range of the species (Bowman et al. 2005). Similarly, eastern chipmunk density was significantly higher in 2003 than in 2002 or 2004 ($P < 0.001$; mean MNKA/ha [$\pm$ SE] = 2.98 [0.55], 7.16 [0.63], and 0.90 [0.28] for 2002, 2003, and 2004, respectively). In pine stands, eastern chipmunk densities in 2004 were significantly lower than in 2002 and 2003 ($P = 0.048$; mean MNKA/ha [$\pm$ SE] = 4.20 [1.51], 5.20 [0.88], and 1.16 [0.51] for 2002, 2003, and 2004, respectively). In contrast, red squirrel densities were significantly high in 2004, compared with densities in 2002 or 2003 ($P=0.025$; mean MNKA/ha [$\pm$ SE] = 0.33 [0.12], 0.17 [0.05], and 1.08 [0.46] for 2002, 2003, and 2004, respectively).

Partial harvesting appeared to have little effect on densities of southern flying squirrels or eastern chipmunks. Densities of both species were slightly higher in cut sites of both ages than in old-forest stands, although not significantly so for either the hardwood or the white pine stands ($P > 0.120$; Table 2). In pine sites, both northern flying squirrels and red squirrels had significantly higher densities in old-forest sites than in recent cuts (Table 2). However, there was a significant interaction between trap year and logging history ($P < 0.001$) for red squirrels because of especially high abundances in old-forest stands in 2004 compared with 2002 and 2003. We did not perform any analyses for northern flying squirrels or red squirrels in hardwood stands because of low captures.

In both hardwood and pine sites, logging history changed the habitat structure present (Table 3). In hardwood sites, 6 habitat variables were significantly higher in old-forest sites than in either age of cut sites: basal area, spruce stems/ha ≥ 25 cm dbh, total conifer stems per hectare, conifer stems/ha ≥ 25 cm dbh, total snag stems per hectare, and snag stems/ha ≥ 25 cm dbh. Stems per hectare of hardwood trees ≥ 25 cm dbh were significantly higher in old-forest stands than in recent cuts. In pine sites, 5 habitat variables were significantly higher in old-forest sites than in recently harvested sites: basal area, canopy closure, total conifer, hardwood stems/ha ≥ 25 cm dbh, and snags/ha ≥ 25 cm dbh. Although not significant, stems per hectare of spruce ≥ 25 cm dbh were greater in old-forest sites than in cut sites.

Habitat Associations

Habitat variable reduction.—Eleven habitat variables remained in the site-level hardwood data set after collinearity was reduced to acceptable levels: basal area, canopy closure, conifer density, hardwood density ≥ 25 cm dbh, spruce density ≥ 25 cm dbh, mast density ≥ 25 cm dbh, declining tree density ≥ 25 cm dbh, snag density, understory stem density ≤ 10 cm dbh, volume of DWD ≥ 25 cm dbh, and volume of old decay class DWD. The 9 habitat variables remaining in the pine habitat data set were canopy closure, conifer density, hardwood density, hardwood density ≥ 25 cm dbh, spruce density ≥ 25 cm dbh, mast density ≥ 25 cm dbh, snag density ≥ 25 cm dbh, hardwood understory density ≤ 10 cm dbh, and the volume of recent decay class DWD.

Variance partitioning: site and landscape habitat associations.—In the variance partitioning analysis, site-level factors were more important than landscape-level factors, accounting for nearly twice as much explained variance. The unique site-level variance accounted for 46.4% and 43.7% of the explained variance in the squirrel community (in hardwood and pine sites, respectively), whereas the landscape-level variance accounted for only 22.0% and 22.5%, respectively. The remaining variance (31.6% and 33.8%, respectively) represented joint and unexplained variance.

Species-specific habitat models.—The stepwise regression models compared favorably with those chosen through the AIC_c procedure (Tables 4, 5). We ranked them as the best or second best model in all pine sites; when they were second best, the ΔAIC_c value was ≤ 0.64 . In hardwood sites, in 6 of 7 instances the stepwise model was one of the best 3 models, with ΔAIC_c values of < 1.29 . The only discrepancy was the model for red squirrels in hardwood sites, with the best AIC_c model adding an additional term (snag stems/ha) in comparison to the stepwise model. As a result, below we describe in more detail the results of the stepwise regression analyses, except for red squirrels in hardwood sites, for which we describe the top-ranked AIC_c model instead.

In hardwood forest, southern flying squirrel densities had a negative correlation with several habitat variables, including basal area (Fig. 1b) and conifer stems per hectare ($r = -0.52$,

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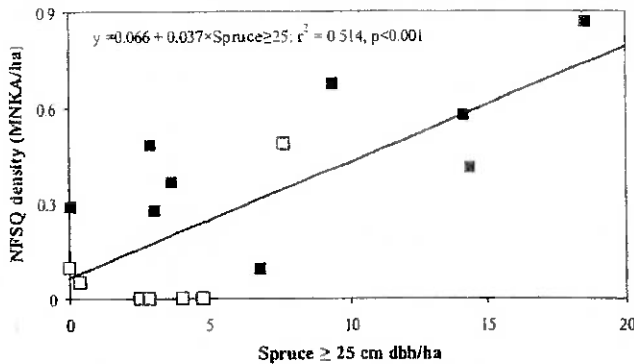


Figure 2. Northern flying squirrel (NFSQ) density in white pine sites in Algonquin Provincial Park, Ontario, Canada, plotted against stems/ha of spruce ≥ 25 cm diameter at breast height (dbh) from summers 2002–2004. Black squares = old-forest sites, empty squares = recent cuts, and the solid line represents the linear regression line.

density and basal area. However, our study measured density, not reproductive success or survival. Taulman et al. (1998) found that predation on radiocollared animals was more frequent in disturbed habitats; similarly, in a concurrent radiotelemetry study, we found that the loss of radiocollared animals was 2.5 times greater in selection cuts than in old-forest stands (Holloway 2006). Open stand structure may lead to easier movement, not only by flying squirrels, but also by their owl predators.

The relationship we observed for southern flying squirrels and snags in hardwood forest was the reverse of our initial predictions. The negative relationship this species showed with snags suggests southern flying squirrels are adaptable in regards to den use. In fact, cavities in live declining trees were the most common den substrate used by southern flying squirrels in our study area (Holloway 2006), and the density of declining trees did not differ between old-forest and cut sites. Mast density is a key habitat feature for southern flying squirrels (Sonenshine and Levy 1981, Bendel and Gates 1987, Taulman et al. 1998), but the availability of this resource appears to influence the spatial scale at which mast is most critical. In suboptimal habitat (mixed conifer–hardwood), mast density was important directly at the local site level. In more suitable hardwood stands, similar to those in Fridell and Litvaitis (1991), we observed a positive relationship between southern flying squirrel density and mast availability on the landscape. Flying squirrels are mobile animals, and presumably move into mast stands during the fall, but a supply of mast must exist either within an animal's home range or in the surrounding vicinity for overwinter survival. Low mast abundance the preceding fall, coupled with cold winter conditions, most parsimoniously explains the crash of the southern flying squirrel population at our study site in 2004 (Bowman et al. 2005).

Chipmunks were ubiquitous across our study sites and partial harvesting had little discernable effect on their populations. Declining trees, dense understory cover, and downed woody debris are important habitat features for eastern chipmunks (Bennett et al. 1994, Mahan and Yahner

1996, Zollner and Crane 2003, this study). Chipmunks use fallen logs and branches as travel runways, while high shrub density provides both protective cover and abundant food. These features in our study area were most abundant in sites with intermediate levels of canopy closure (particularly declining trees). Intermediate canopy closure shows a link to sites with intermediate gap sizes created by less intensive (or older) logging activity, or the mortality of overstory trees, which results in mosaic of gaps in old-forest stands.

This study affirmed the link between high densities of northern flying squirrels and red squirrels and older, undisturbed forests (Carey et al. 1999). Characteristics associated with old-forest areas (high snag density and basal area) were important predictors for these 2 species. Shelterwood harvesting resulted in significantly lower densities of standing trees, spruce, hardwoods, snags, and canopy closure, leading to an overall reduction in structural complexity. The loss of these features under shelterwood harvesting may be problematic for both northern flying squirrels and red squirrels because high structural diversity and overstory cover are associated with decreased predation risk (Vahle and Patton 1983, Carey 2000). Moreover, these changes will affect the availability of nesting habitat because northern flying squirrels and red squirrels commonly use hardwood trees and snags as nests in central Ontario (Obbard 1987, Holloway 2006). Finally, the removal of trees increases the habitat suitability for understory species such as eastern chipmunks at the expense of the arboreal sciurids.

The abundance and availability of foraging resources also may be a critical consideration for these species (Kemp and Keith 1970, Ransome and Sullivan 1997, Carey et al. 1999). Hypogeous fungi are major dietary items for northern flying squirrels and red squirrels, and both species act as primary dispersers of fungal spores (Maser et al. 1986, Vernes et al. 2004). Spruce density was a key habitat predictor for both species, supporting previous research both in the boreal forest and in the southern Appalachians (Fancy 1980, Payne et al. 1989, Cotton and Parker 2000, Ford et al. 2004). Spruce is important directly as a seed source (a major diet item for red squirrels; Kemp and Keith 1970) and indirectly because of its mycorrhizal associations with fungi. In the Appalachians, the presence of truffles was associated with red spruce (*Picea rubra*) abundances (Loeb et al. 2000), and the frequency of ectomycorrhizal fungi occurrence in red spruce stands was double that found in adjacent hardwood stands (Bills et al. 1986). In particular, the most common fungal genus, *Elaphomyces*, found in the Appalachians (Loeb et al. 2000) and in northern flying squirrel feces in this study (Holloway 2006), was associated with spruce (*Picea* sp.) and fir (*Abies* sp.) trees.

In addition to a reduction in spruce and snag densities, shelterwood harvesting may also decrease the microclimatic suitability in stands for fungi. Hypogeous fungal productivity is associated with old-growth features (such as a well-developed organic soil layer, abundant coarse woody debris, and the presence of large, old trees; North et al. 1997). The

abundance of flying squirrels and hypogeous fungi was significantly lower in shelterwood stands than in uncut old-growth stands in California (Waters and Zabel 1995). Beyond the local site-level effects of harvesting, we observed additive effects of logging on the surrounding landscape. This suggests that the interspersed of large harvested and unharvested blocks on the landscape may be important to ensure the persistence of red squirrels and northern flying squirrels.

We developed habitat models using both stepwise regression and models developed a priori. Stepwise regression has fallen into disfavor recently because of misuse of the technique (excessive data dredging), its reliance on arbitrary cutoffs (e.g., $\alpha = 0.05$), and model over-fitting (Burnham and Anderson 1998, Stephens et al. 2005). However, models developed a priori may be equally prone to problems when considering a large number of potential variables (i.e., model dredging; Stephens et al. 2005). Thoughtful model development is critical in both stepwise techniques and a priori model building. If researchers take care in developing models, we believe stepwise regression is a powerful tool and should continue to be used in habitat studies. Habitat studies often lead to the development of large sets of potential variables, and the inclusion of novel variables can lead to new insights.

Management Implications

Shelterwood harvesting decreased the density of large spruces and hardwoods below critical thresholds for north-

ern flying squirrels and red squirrels. In order to mitigate the structural changes resulting from logging, we recommend managers retain at least 4.5 spruce trees/ha ≥ 25 cm dbh and 15 hardwood trees/ha ≥ 25 cm dbh in white pine stands (levels predicted to maintain northern flying squirrel densities in shelterwood stands at 50% of their mean level in old-forest areas). The abundance of mast trees on the landscape appears to limit southern flying squirrel density. In hardwood stands, we recommend foresters maintain a minimum of 17% of the landscape area (to maintain 80% of their mean level in hardwood forests) with high mast tree abundance (i.e., where $\geq 20\%$ of the stand composition is a mast tree).

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LIFE AFTER DEATH

The amazing productivity of dead trees, both standing and fallen. *By Ellen Horowitz*

High on a ridgetop, the silver skeleton of a wind-scoured pine beckoned. As I walked beneath its thick, gnarly branch stubs, my hand followed the sleek contours of the tree's twisted trunk until I came upon an old woodpecker hole. It was late summer, nesting season was long over, and I couldn't resist the temptation to ask, "Hello, is anybody home?" Feeling certain no one was, I followed the question with a gentle knock. The unexpected answer—a bat—shot out of the hole.

I don't know who was more surprised—the bat or me—but that long-ago moment still reminds me of just how many animals rely on dead trees. In Montana, more than 60 species of wildlife use dead trees or logs for feeding, nesting, roosting, resting, denning, or drumming.

Standing dead trees (commonly called snags) and downed logs are the overlooked and underappreciated life-giving parts of any forest. Living trees with heart-rot decay,

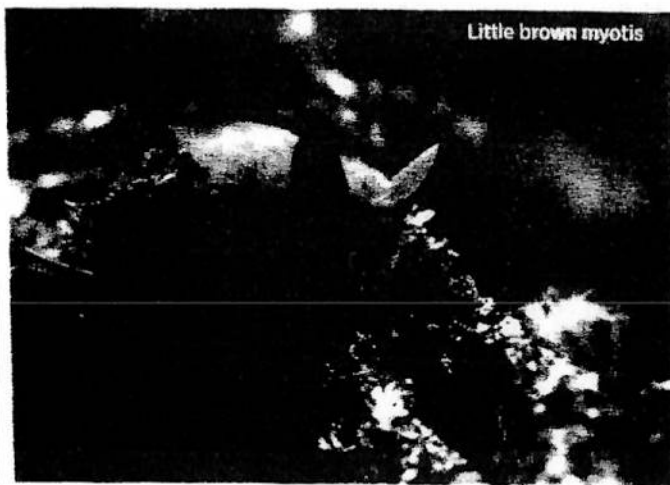
broken or dead tops, and large dead branches also function as snags. And they too can be filled with wildlife.

Everyone knows that healthy live trees are wonderful for wildlife. Birds nest in their branches, insects eat the leaves, and the trees convert carbon dioxide into oxygen that all life on earth needs. What makes dead trees so valuable to wildlife are the small and large holes and cavities that provide shelter for birds, squirrels, bats, and even bears. Openings also allow moisture and fungi to get inside the structure and trigger rot and decay that attract insects eaten by wildlife.

"Believe it or not, a dead tree often holds more living creatures than a similar-size live tree," says Torrey Ritter, regional nongame wildlife biologist for Montana Fish, Wildlife & Parks in Missoula.

Woodpeckers, with their chisel-like bills, are renowned for drilling holes in trees, which they and other wildlife use for roosting and nesting. Fungi that cause decay also create cavities that house dozens of species. These openings can range in size from small knot-holes to entire hollow trees. Almost any injury to a tree's protective bark—caused by fire scars, lightning strikes, storm damage, insects, antler rubs, bears, and humans—can produce openings for ecologically essential fungal spores.

Fungi perform the critical job of decomposing and recycling forest nutrients. Some mycorrhizal fungi transport nutrients to trees and other plants to help



Little brown myotis



LEFT TO RIGHT: JEREMY HOLMAN, GARY KRAMER

PREDATORS' PREFERENCE Forest carnivores like American martens (above) and fishers den in fallen tree cavities and pre on small mammals attracted to logs.



ORGANIC MATTER EATERS Centipedes, millipedes, sow bugs (above), slugs, snails, earthworms, and a wide range of insects, such as earwigs, ground beetles, and spring-tails, are detritivores that eat dead trees and provide food for birds and other wildlife.

mistakenly blamed for eating trees, are simply taking advantage of easy digging within a log or stump's soft, fungus-infested heartwood to build their nests. In the forest, carpenter ants play a beneficial role by preying on other insects and recycling organic matter. They also provide protein-rich food for pileated woodpeckers and bears.

Another thing logs do is soak up water

like a sponge, helping them retain moisture even during summer drought. Salamanders, rubber boas, and boreal toads burrow or shelter beneath the cool, moist logs to wait out the heat of the day.

Finally, logs turn into soil. Slowly decomposing over the course of decades or centuries, the downed tree trunks enrich the forest floor while supporting the growth of lichens, mosses, and mushrooms on their surfaces. In moist forests, they serve as nursery logs, providing seedbeds for other plants, including trees, to get their start

"Dying and dead wood provides one of the...greatest resources for animal species in a natural forest," wrote Charles S. Elton, a British ecologist and contemporary of Aldo Leopold. "[If] fallen timber and slightly decayed trees are removed, the whole system is gravely impoverished of perhaps more than a fifth of its fauna."

The next time you come upon snags while walking through the woods, don't mourn for the dead trees. Celebrate the life those vital habitats are giving to wildlife today—from songbirds to black bears—and will continue to give, even when toppled and decayed, far into the forest's future. 🐻



Even trees grow from old, dead trees, completing a full circle of forest life.

Hollow homes

A "hollow" tree is defined as one with such advanced decay throughout its interior heartwood that a hollow core forms. Biologists consider large-diameter (20-plus inches) hollow trees especially useful to wildlife. Studies in northeastern Oregon indicate that roosting and nesting Vaux's swifts require a tree averaging 27 inches wide and 85 feet tall. Hollow treetops for denning black bears average more than 43 inches wide and 57 feet high.

Hollow snags and hollow logs always start with a live tree. The hollowing process begins when the live tree is damaged. Strong winds, for example, may snap off a treetop or large branch, exposing it to airborne heart-rot fungal spores. Deep fire scars at the tree base can also create an opening for fungal spores. These fungi do their work only in live trees.

After many decades, the decayed heartwood detaches from the sapwood, resulting in a hollow chamber. Since the live outer sapwood isn't affected, the tree retains its hard, protective shell while continuing to grow. In other words, a tree can be hollow and still very much alive.

Because they look intact from the outside, hollow trees can be tough to identify unless there's an obvious opening. But they are worth finding, because these trees always house some sort of wildlife. Look for live trees with:

- ▶ a broken top.
- ▶ evidence of multiple pileated (or other) woodpecker cavities.
- ▶ appearance of shelf fungi close to branch stubs or live branches, or
- ▶ hollows (knotholes) where large branches have broken off. ■



A black bear peers out from its den in a hollow log.



Scan the QR code at left to see a sleepy black bear emerging after hibernation in a large Glacier National Park snag cavity.

Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire

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Abstract. We conducted bird surveys in 10 of the first 11 years following a mixed-severity fire in a dry, low-elevation mixed-conifer forest in western Montana, United States. By defining fire in terms of fire severity and time-since-fire, and then comparing detection rates for species inside 15 combinations of fire severity and time-since-fire, with their rates of detection in unburned (but otherwise similar) forest outside the burn perimeter, we were able to assess more nuanced effects of fire on 50 bird species. A majority of species (60%) was detected significantly more frequently inside than outside the burn. It is likely that the beneficial effects of fire for some species can be detected only under relatively narrow combinations of fire severity and time-since-fire. Because most species responded positively and uniquely to some combination of fire severity and time-since-fire, these results carry important management implications. Specifically, the variety of burned-forest conditions required by fire-dependent bird species cannot be created through the application of relatively uniform low-severity prescribed fires, through land management practices that serve to reduce fire severity or through post-fire salvage logging, which removes the dead trees required by most disturbance-dependent bird species.

Additional keywords: Black-backed Woodpecker, conifer forest, ecological integrity, fire severity, mixed-severity fire, restoration, salvage logging, wildfire.

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Introduction

The earliest synthesis of fire effects on birds (Kotliar *et al.* 2002) revealed that many species respond positively, others negatively and still others in a mixed fashion to burned forest conditions. Perhaps the most important pattern that emerged from this synthesis is that some species (the more extreme including the American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*Picoides arcticus*), Mountain Bluebird (*Sialia currucoides*) and Tree Swallow (*Tachycineta bicolor*)) are relatively abundant in burned forest conditions. One (the Black-backed woodpecker) is even relatively restricted in its distribution to such conditions. For example, Hutto (1995) reported that 15 species were more abundant in burned forests than they were in any of the other 14 vegetation types included in his meta-analysis. This carries important management implications because those species may depend to a large extent on fire to create the habitat conditions they need for persistence – habitat conditions that are severely compromised by fire prevention, fire suppression, and post-fire salvage logging, seeding, tree planting and removal of native shrubs (Saab and Dudley 1998; Kotliar *et al.* 2002; DellaSala *et al.* 2006; Hutto and Gallo 2006; Hutto 2008; Saab *et al.* 2009; Swanson *et al.* 2011; DellaSala *et al.* 2014; Tingley *et al.* 2014).

Until very recently, studies of fire effects did not distinguish the effects of low-severity, mixed-severity and high-severity fires. Therefore, reported responses of species were oftentimes different from one study to the next, and terms like ‘mixed responder’ were included in tables generated from synthetic work on fire effects (Kotliar *et al.* 2002). Kotliar *et al.* (2005) noted that fire severity, time-since-fire, vegetation type and other considerations could probably explain some of the variation among studies, but it was not until Smucker *et al.* (2005) characterised the severity of the fire surrounding each of a series of survey points that bird responses to fire became much less ambiguous and remarkably consistent. Smucker *et al.* (2005) proposed that most bird species respond predictably to fire, but that the type of response (positive or negative) depends strongly on fire severity. Subsequently, numerous studies (e.g. Covert-Bratland *et al.* 2006; Kirkpatrick *et al.* 2006; Conway and Kirkpatrick 2007; Koivula and Schmiegelow 2007; Kotliar *et al.* 2007; Hanson and North 2008; Kotliar *et al.* 2008; Vierling and Lentile 2008; Nappi *et al.* 2010; Nappi and Drapeau 2011; Dudley *et al.* 2012; Fontaine and Kennedy 2012; Lee *et al.* 2012; Lindenmayer *et al.* 2014; Rush *et al.* 2012; Hutto *et al.* 2015; Stephens *et al.* 2015) have demonstrated a marked effect of fire severity on either the occurrence or breeding success of selected

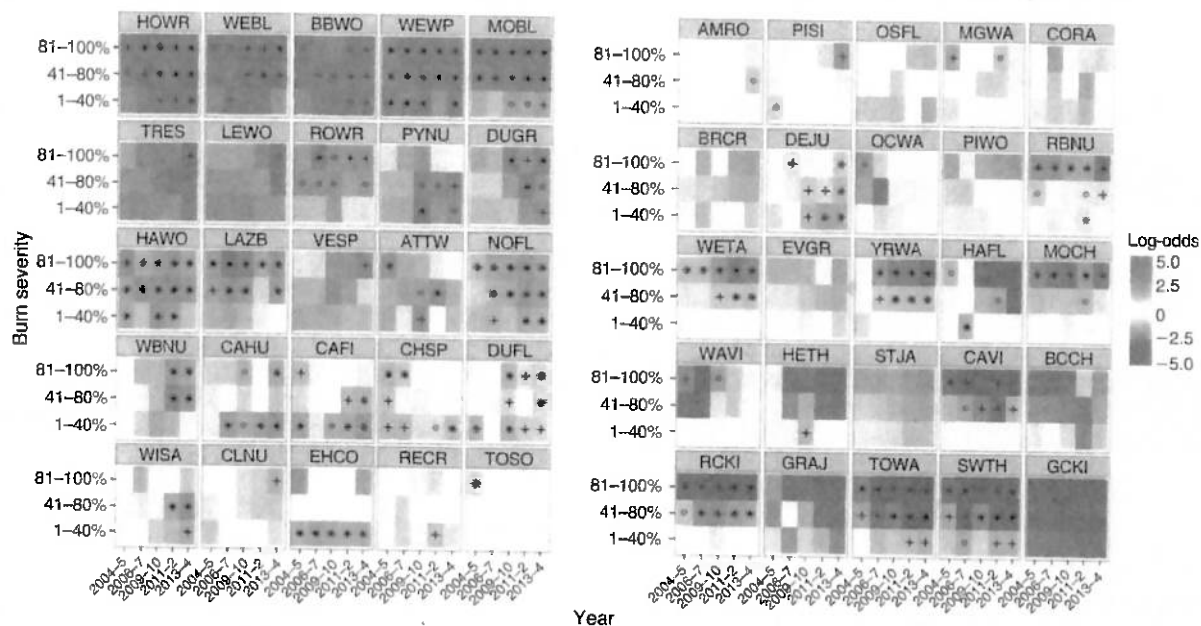


Fig. 2. Heat maps reflecting the log-odds ratio associated with the percentage occurrence in each combination fire severity and time-since-fire in comparison with the percentage occurrence in unburned forest outside the fire perimeter for each of 50 bird species (four-letter mnemonic codes provided in Table 2; species are organised by their average log-odds scores, from those that had a large average positive response to those that had a large average negative response to fire). Hotter (more red) blocks represent positive responses to fire and cooler (more blue) blocks represent negative responses to fire. The symbols correspond with Bonferroni adjusted P -values ($\diamond = 0.01 < P < 0.05$; $+$ = $0.001 < P < 0.01$; $*$ = $P < 0.001$). Thirty of 50 species (60%) were significantly more abundant in burned forest at some combination of severity and time-since-fire than in unburned, mature green-tree forest.

Golden-crowned Kinglet (*Regulus satrapa*) were detected less frequently after fire, regardless of fire severity, and their detection rates generally continued to decrease over time (Fig. 2).

Discussion

Following the most common approach to assessing fire effects, we first looked at whether there were significant differences in bird abundances between the burned and surrounding unburned forest. The results from this analysis were consistent with those reported in many other studies of fire effects on birds (see Kotliar *et al.* 2002) – roughly half the bird species appeared to benefit and half did not (Table 2). Unfortunately, this kind of analysis hid positive responses that became apparent only after accounting for fire severity and time-since-fire. By dividing the burned-forest data into 15 combinations of fire severity and time-since-fire, we found results that were more nuanced than those obtained from a simple ‘burned vs unburned’ analysis. Specifically, 30 of 50 (60%) of the bird species considered were significantly more likely to occur inside the burned forest (at 1 or more combinations of fire severity and time-since-fire) than outside the burned forest. The distinct location of the greatest probability of detection for any 1 species across the 2-dimensional fire-severity and time-since-fire gradient, combined with differences in those locations among species (Fig. 2), suggests that the bird occurrence patterns are accurate reflections of bird abundance and not artefacts of some kind of sampling bias that might affect all species similarly. Other recent work (Stephens *et al.* 2015) has also revealed that the locations

of peak abundances across a fire-severity/time-since-fire gradient differ among species.

Many of these significantly positive responses would not have been evident without partitioning the data into multiple severity and time-since-fire categories. This kind of analysis is difficult to conduct with data from any one fire because sample sizes (the number of independent survey points in each severity-by-year category) are generally much smaller than what we were able to achieve here (Table 1). Even with the sample sizes we achieved, we were still forced to use fewer categories than the number used in the field to assess the statistical significance of fire effects. Although each bird species responded uniquely to the combination of fire severity and time-since-fire (Fig. 2), four general classes of response are worth noting, along with some of the most probable biological underpinnings behind each.

Response Pattern 1

This pattern is illustrated by species that showed an abrupt increase in abundance within the first few years following fire, and the elevated abundance persisted until the end of the 11-year study primarily (but not exclusively) in locations that burned at higher severities. Several woodpecker species (Black-backed Woodpecker, Hairy Woodpecker, American Three-toed Woodpecker and Northern Flicker) showed this response pattern (Fig. 2). The biological basis behind the abrupt increase in woodpecker populations is well established and unambiguous: bark and wood-boring beetle populations increase as individual beetles detect the newly created abundance of fire-killed trees.

In turn, developing larvae provide food for woodpeckers, which then respond numerically with an abrupt increase in abundance during the first year or two after fire. Relatively rare species like the American Three-toed and Black-backed woodpeckers are known to appear within months after fire (Blackford 1955; Villard and Beninger 1993; Villard and Schieck 1997). Their abundances then increase at a rate that is more rapid than expected if the increase were entirely the result of recruitment from inside the burn, so the increases are undoubtedly associated with colonisation by birds from outside the burned area, as others have noted (e.g. Van Tyne 1926; Koplin 1969; Yunick 1985; Hoyt and Hannon 2002; Huot and Ibarzabal 2006; Siegel *et al.* 2016). Perhaps the most iconic indicator of a severely burned mixed-conifer forest throughout the Sierra Nevadas of California, the Intermountain West and Canadian boreal forest is the Black-backed Woodpecker (Hutto 1995; Hanson and North 2008; Hutto 2008; Hutto *et al.* 2008; Nappi and Drapeau 2009; Swanson *et al.* 2011; Bond *et al.* 2012; Hutto *et al.* 2015). Although its pattern of response to fire is not much different than that of the American Three-toed Woodpecker, Hairy Woodpecker or Northern Flicker (Fig. 2), the key difference between this woodpecker and the others lies with the extent to which the species is restricted in its distribution to burned forest conditions. Other woodpecker species occur in green-tree forests to a much greater extent than the Black-backed Woodpecker; hence, the Black-backed Woodpecker is a better 'indicator' of severely burned forest conditions. The relatively high Black-backed Woodpecker occurrence rates across an 11-year period is somewhat surprising given the existing literature (Apfelbaum and Haney 1985; Hutto 1995; Murphy and Lehnhausen 1998; Hobson and Schieck 1999; Hoyt and Hannon 2002; Saab *et al.* 2007), which suggests that a 4–8-year window of opportunity is about all one can expect for this species before they begin to decline in abundance. It may very well be that the mixed-severity fire allowed this species to persist longer in this study than in most others because there was an abundance of weakened trees in the moderate- to low-severity border areas, which continued to provide adequate food resources after conditions in the more severely burned portions became less suitable. This mechanism of persistence beyond durations expected on the basis of averages gleaned from the literature has been suggested to operate elsewhere as well (Nappi *et al.* 2010; Dudley *et al.* 2012).

Other bird species (e.g. Cassin's Finch; Clark's Nutcracker, *Nucifraga columbiana*; Red Crossbill; Pine Siskin) that appear to respond abruptly and positively to more severe fire, do so for reasons that are most likely related to the abrupt increase in availability of seeds that are retained in cones that open in response to fire. Still other species in this group respond quickly to what is probably an increase in the availability of the combination of nest sites associated with standing-dead trees and open areas for foraging either on the ground (e.g. Western Bluebird and Mountain Bluebird) or in the air (e.g. Western Wood-Pewee) or to an increase in the availability of relatively predator-free nest sites at ground level from burned-out roots and root wads associated with wind-thrown trees (e.g. Rock Wren; Townsend's Solitaire; Dark-eyed Junco, *Junco hyemalis*). The Olive-sided Flycatcher (*Contopus cooperi*) makes special use of nest sites that are located in green-needled or

brown-needled trees on the edges of severely burned forest where they can sally into the openings created by crown fire.

Response Pattern 2

This pattern is illustrated by species that showed a slightly delayed increase in abundance, primarily (but not necessarily) in locations that burned at higher severities. If we had confined the study to the first year or two after fire, these positive responses to fire would have gone undetected. One of these species (Vesper Sparrow) appeared after a brief delay in the development of suitable grass-dominated patches, while several others (e.g. Dusky Grouse; Lazuli Bunting; Orange-crowned Warbler, *Oreothlypis celata*) were probably responding to the development of suitable shrub and seedling layers for foraging and nesting, which varied markedly from one place to another within the burn perimeter. Still other species (e.g. House Wren, *Troglodytes aedon*; Lewis's Woodpecker; Tree Swallow; Williamson's Sapsucker) were probably responding to a delayed increase in the availability of cavity nest sites that became available either after they were excavated by woodpeckers soon after fire or after the larger standing-dead trees began to soften with decay and break more easily in wind events. The House Wren clearly benefitted from tree blowdown and breakage events that occurred in the first 6 years after fire; its abundance grew steadily to the point that it was the most abundant species in severely burned forest patches 6–11 years after fire.

Several authors (e.g. Hutto 1995; Gentry and Vierling 2007; Saab *et al.* 2007) have recognised a delayed increase in populations of Lewis's Woodpecker following severe fire, and it is clear that the benefit of severe fire to this woodpecker species would not have been detected in this study had the data collection period been restricted to the first few years after fire. The delayed positive responses of other species (e.g. Williamson's Sapsucker and White-breasted Nuthatch) have not been described previously and they are notable, as we discuss more fully below. Williamson's Sapsucker is noteworthy in that its distribution was nearly restricted to edge conditions between unburned forest patches (where it fed on sap of living trees) and adjacent burned forest patches (where it nested in relatively large, decayed or broken-topped trees that became abundant after wind events in severely burned patches created them a decade or so after fire). The delayed increase in White-breasted Nuthatch detections may be related to the increase in availability of insects beneath thick bark after the bark began to peel away from, or slough off, dead Ponderosa Pine, Western Larch, and Douglas-fir. Finally, the delayed increase by Western Bluebird represents a pattern that has received considerable attention (Duckworth and Badyaev 2007; Duckworth 2008, 2009; 2010, 2012; 2014); Western Bluebirds are not as well adapted as Mountain Bluebirds are to colonise burned forests early on after fire, but once they colonise, they are better suited to outcompete the Mountain Bluebird in severely burned hot spots.

The pattern of a rapid increase in abundance illustrated by species listed under the first response pattern is well described and well appreciated, but the second pattern of a delayed increase in severely burned forest patches is not widely appreciated because the use of a single 'after fire' category in many

previous fire effects analyses may have hidden the influence of a delayed response. For example, of the 11 published studies of bird communities in burned and unburned forests reviewed by Kotliar *et al.* (2002), none separated the effects of fire severity or time-since-fire. Since that time, numerous authors (Hannah and Hoyt 2004; Saab *et al.* 2004; Smucker *et al.* 2005; Kirkpatrick *et al.* 2006; Schieck and Song 2006; Kotliar *et al.* 2007; Saab *et al.* 2007; Hutto 2008; Kotliar *et al.* 2008; Pons and Clavero 2010; Nappi and Drapeau 2011; Saracco *et al.* 2011; Stephens *et al.* 2015) have included either fire severity or time-since-fire in their analyses of fire effects, and all of these authors concluded that it is important to do so. This study serves to reinforce the idea that fire effects cannot be accurately assessed in the absence of knowledge about the context surrounding a particular sample location and that includes, but is not limited to, fire severity and time-since-fire.

Response Pattern 3

This pattern is illustrated by species that revealed a fairly abrupt or slightly delayed increase in abundance within the first year or two following fire, but the positive response is limited to locations that burned at lower severities. This group includes species that have previously been labelled as 'mixed' responders in meta-analyses of fire effects (e.g. Kotliar *et al.* 2002) because they respond positively to fire in some studies and negatively to fire in others. Our results suggest instead that these species do not respond to fire unpredictably; it is just that their response depends on fire severity. For example, some of these species maintained an elevated occurrence rate in locations that burned at a lower severity throughout the duration of the 11-year study (e.g. Brown-headed Cowbird, Red Crossbill, Red-breasted Nuthatch, Western Tanager and Ruby-crowned Kinglet), while others showed a positive but brief response to low-severity fire only for a brief period following fire (e.g. Common Raven; Brown Creeper, *Certhia americana*; Pileated Woodpecker; Evening Grosbeak; Yellow-rumped Warbler; Hammond's Flycatcher; Hermit Thrush). For those species that showed a sustained (albeit small) positive response to low-severity fire, a predominantly green-tree forest that burned recently at low severity might actually provide a forest condition that is more suitable than a long-unburned green-tree forest. The species that revealed a brief and limited increase in abundance only during the first year or two following fire may reflect an influx of individuals returning from wintering locations only to find many of their previously occupied locations too severely burned, so they then proceeded to squeeze into unburned or lightly burned forest near previously occupied forest patches. If true, their relatively high abundance in mildly burned forest may not reflect suitable conditions, but may be a reflection of birds making the best of a bad situation. A key question for future fire research would be to determine whether increases in numbers of detections after recent fire in mildly burned green-tree stands reflect conditions that are better in quality, even if only briefly, than long unburned green-tree stands for this group of species.

Response Pattern 4

This pattern is illustrated by the six species that were less abundant in burned than in unburned forest immediately

following fire and appeared to become even less abundant across the 11-year time span. For each of these species, there was no combination of fire severity and time-since-fire that resulted in detection rates that were as great as they were in unburned forest. Perhaps these species do not benefit in any way from fire. Indeed, many authors would be quick to classify the species associated with this group of six species as 'negative responders.' However, we know that the abundances of each of these six species will be lower in recently burned forests only in the short-term. This was only an 11-year study, and we know that these same species will reach their highest occurrence rates in the years to come. If those occurrence rates reach a peak at some point in the future before falling again when the forest reaches an even older age, then those species would also be more accurately classified as positive responders; it is just that the time required to show a relatively high abundance is longer than the length of the present study. Even a rudimentary knowledge of natural history suggests that many bird species (e.g. Orange-crowned Warbler, MacGillivray's Warbler, Calliope Hummingbird and Lazuli Bunting) benefit from high-severity fire, but the greatest positive response cannot usually be detected until somewhere between 10 and 30 years following severe fire when plant succession produces a high density of conifer seedlings and shrubs. Similarly, the six species in this last group could be said to benefit from fire if forest conditions associated with, hypothetically, a 300-year-old forest are not as good as forest conditions associated with a 100-year-old forest because the only way optimal conditions for these species could be 'restored' would be through a severe fire event that creates their preferred habitat 100 years later. Interestingly, Taylor and Barmore (1980; Table 2) showed precisely that pattern for Ruby-crowned Kinglet, Yellow-rumped Warbler and Hermit Thrush in Yellowstone and Grand Teton National Parks – those species that are more abundant in century-old than in either younger or older forests. Using the same logic, even a species that is more abundant at year 300 than at year 700 following fire would mean that severe disturbance (disturbance severe enough to trigger ecological succession) is necessary to 'restore' appropriate forest conditions for that species too (see also Imbeau *et al.* 1999, Schieck and Song 2006; Zhao *et al.* 2013). The important point is that we cannot assess the effects of fire without data on bird abundances from a more extended series of forest ages following fire.

Caveat and management implications

Because the bird occurrence rate at unburned points was based on a different set of years than the occurrence rate for any one of the two-year post-fire samples, it is possible that a significant difference in the abundance of any one species between the unburned and a particular fire severity/time-since-fire category resulted from a temporal change in abundance independent of fire effects. However, even though our results emerged from a single fire event that may be best considered a case study, a previous study of bird occurrence patterns across hundreds of fires over the past 30 years (see Hutto *et al.* 2015, and references therein) suggests that the individual species' responses make good biological sense and are not artefacts of unusual increases or declines in bird abundance independent of fire effects. Nonetheless, these findings should serve as hypotheses to be

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tested through replication of independent samples drawn from different time-since-fire categories. Only through use of a chronosequence approach (Hutto and Belote 2013) will we be able to generate the replication of burned-forest conditions necessary to evaluate fire effects in a manner that will allow us to appreciate how both fire severity and time-since-fire create the conditions needed by birds that respond positively to fire.

The take-home lesson here is that we cannot rely on traditional 'burned vs unburned' comparisons presented in most published reports on fire effects to assess whether species respond positively or negatively to fire. Fire severity, time-since-fire and other forest conditions matter to organisms that respond positively to disturbance, therefore we will have to consider the kind of forest, tree sizes and densities, fire severity and time-since-fire if we want to investigate fire effects in a biologically meaningful way. By considering the effects of just two of those forest conditions here, it is clear that the majority of species increases in abundance during part or all of the first dozen years after fire, as evidenced by significant differences in rates of detection inside vs outside burned forests. Thus, we cannot gain a thorough understanding of fire effects through results that emerge from short-term, before-and-after studies; we need to know more about the occurrence rates of species across very long time spans if we are to speak knowledgeably about the effects of fire on any particular species. Our finding that 60% of the bird species surveyed are most abundant in some stage of forest succession following fire than they are in mature forest is undoubtedly a conservative estimate of the proportion of species that benefit from fire because our data cover only a relatively short 11-year period following fire.

Not only are there unambiguous responses by the majority of bird species to fire, but the responses are also highly dependent on a spatial component associated with fire severity. As suggested by earlier work that included fire severity as an independent variable (e.g. Smucker *et al.* 2005; Kotliar *et al.* 2007, 2008; Vierling and Lentile 2008; Stephens *et al.* 2015), fire severity has a dramatic influence on the probability of occurrence of bird species. The same pattern was true here for nearly all species that were detected on at least 10 points. Some species are clearly most abundant in the less severely burned forest patches, while others are clearly most abundant in the more severely burned patches. This result is important because it implies that mixed-severity fire effects are necessary for the creation of conditions needed by the variety of bird species that respond positively to fire. Even more importantly, the variety of burned-forest conditions favoured by different bird species may be difficult to create through a prescription of low-severity understory fire applied outside the normal fire season, because such fires do not generate the higher-severity patches needed by the species that are relatively restricted to forests that have burned severely (Hutto 2008). In addition, land management practices designed to prevent or eliminate severe fire will also eliminate the very conditions required by many of the species highlighted here, as will post-fire salvage logging, which has been documented to have overwhelmingly negative effects on birds – effects that are among the strongest and most consistent scientific results ever published on any wildlife management issue (Hutto *et al.* 2015).

Ecologists have long known that severe, stand-replacement fires are characteristic of some (mostly subalpine) forest types

(Brown and Smith 2000), but many forest managers and most politicians along with the public at large are still remarkably uninformed about the naturalness and necessity of severe fire in vegetation types born of, and maintained by, severe fire (Hutto *et al.* 2016). Even more striking is the near absence of an appreciation for the naturalness and necessity of severe fire in the low- to mid-elevation mixed-conifer forest types, even though severe fire events that create patches of severely burned forest are a natural and important part of those forests too (Baker *et al.* 2007; Hessburg *et al.* 2007; Baker 2009; Margolis *et al.* 2011; Perry *et al.* 2011; Baker 2012; Heyerdahl *et al.* 2012; Marlon *et al.* 2012; Veblen *et al.* 2012; Williams and Baker 2012a, 2012b; Odion *et al.* 2014; Sherriff *et al.* 2014; Williams and Baker 2014; Baker 2015a, 2015b; Baker and Williams 2015; Yocom-Kent *et al.* 2015; Hutto *et al.* 2016). For the lower-elevation mixed-conifer forest types, such as the forest studied here, it is quite clear that some amount of severe fire is natural and that large numbers of bird species benefit from the severe-fire component. Given these results, the challenge is to educate land managers, politicians and the public at large about the importance of maintaining severe fire on the landscape and to design fire-safe communities that can withstand the effects of severe fire disturbance events (Hutto *et al.* 2016). Only then will we be in a position to manage for appropriate amounts and sizes of severely burned forest patches that occurred historically and to celebrate the creation of mosaics of different fire severities and post-fire ages that follow directly from severe fire as a natural disturbance process.

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Temperature changes wreak havoc in deforested areas

By Trent Knoss • Feb. 22, 2016



A clear-cut forest area near Eugene, Oregon. Photo by Calibas / Wikipedia.

The newly exposed edges of deforested areas are highly susceptible to drastic temperature changes, leading to hotter, drier and more variable conditions for the forest that remains, according to new research from the University of Colorado Boulder.

The findings suggest that thermal biology—an emerging discipline that examines the effects of temperature on biological and ecological processes—could be an effective tool for understanding

how temperature changes in fragmented habitats can potentially wreak havoc on species activity and other critical ecosystem functions.

A study outlining a framework for applying thermal biology to deforestation research was recently published in the journal *Ecology Letters*.

Previous research has shown that widespread deforestation is a threat to global biodiversity, but scientists are only just now beginning to examine the role that temperature may play when trees are removed from an ecosystem—especially near the newly-cut edges of forests.

“When you chop down trees, you create hot spots in the landscape that are just scorched by the sun,” said Kika Tuff, a PhD candidate in the Department of Ecology and Evolutionary Biology at CU-Boulder and the lead author of the new paper. “These hot spots can change the way that heat moves through the landscape.”

In some cases, this creates a phenomenon known as the ‘vegetation breeze,’ where low air pressure in the cleared areas pulls the cool, moist air out of the forest and feeds hot, dry air back in.

“So now the cleared areas get all the rain and the forests gets sucked dry,” said Tuff.

The warming effect is most pronounced between 50 and 100 meters of a forest edge, the study reports, where

temperatures can be anywhere from 4 to 18 degrees Fahrenheit warmer than in the forest interior.

“This is like climate change on steroids,” Tuff said, “and it happens over much more rapid time scales.”

Biologists estimate that 20 percent of the world's remaining forests lie within 100 meters of an edge, while more than 70 percent lie within a kilometer of one. This means that much of the world's forests may be experiencing the vegetation breeze and other warming effects.

Increased temperature variation near forest edges could affect species' ability to regulate their body temperatures, resulting in behavioral changes that could alter the local ecosystem.

One such example, Tuff said, could be the feeding patterns of animals living at the forest edge. Animals are very temperature sensitive, so they hunt for food when they have sufficiently warmed up in the morning and stop hunting for food when it is too hot in the afternoon. If temperatures are



Kika Tuff

higher at the forest edge, species may respond by retreating to hunt in the cooler, deeper forest, where they become dependent on new types of food, sparking a domino effect in the food chain.

Another example might be the timing and duration of species activity. If temperatures were to increase due to tree loss, predators may start foraging later in the day to avoid the heat. Such a change could increase how frequently predators come across their prey, intensifying predation events and resulting in localized prey population crashes in some cases.

Such effects should also apply in instances of natural treefall, Tuff said. In Colorado, for example, high winds, wildfires and beetle kill can create edges in the treeline where greater sunlight exposure would subsequently increase the solar radiation and temperature in localized areas.

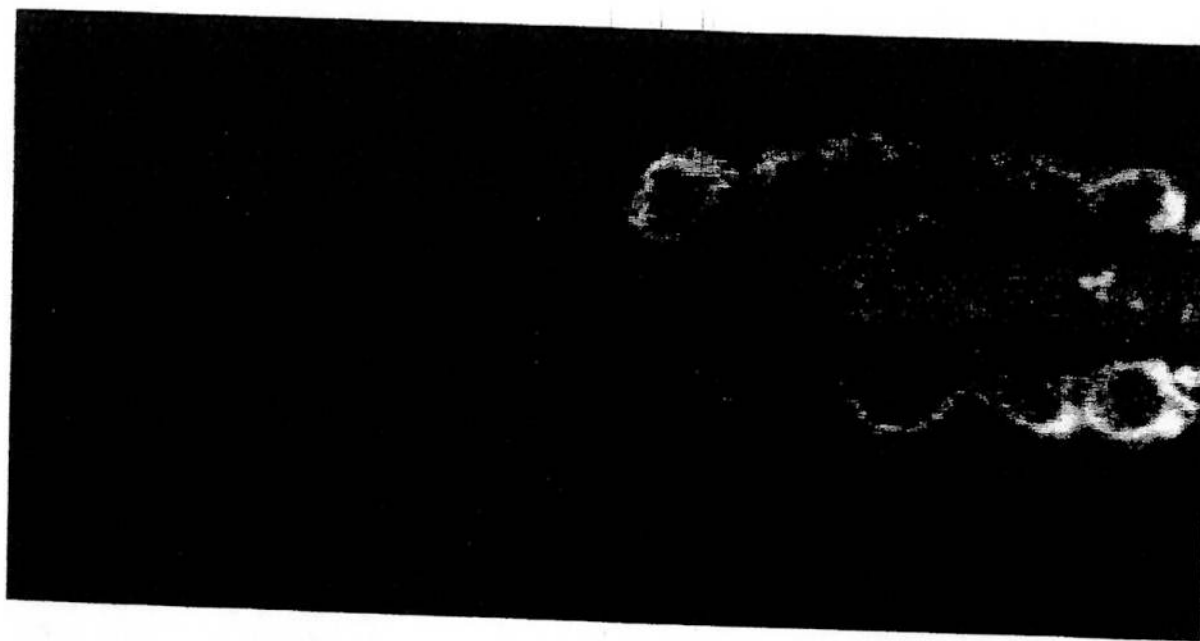
The sensitivity of animals and plants to temperature could have implications for future conservation strategies as deforestation and habitat fragmentation continue worldwide.

"Applying thermal biology on the scale of landscapes is a fairly new idea," Tuff said. "Thermal biology presents a new imperative for forest conservation and makes the value of forests all the greater because of what they do for thermal regulation. Trees aren't just habitat for animals, they are the world's insurance for a thermally stable and habitable planet."

The study was co-authored by Assistant Professor Kendi Davies and graduate student Ty Tuff, both of the Department of Ecology and Evolutionary Biology (EBIO) at CU-Boulder.

Trent Knoss is a science editor at the CU Office of News Services.

Related Articles



[Gene controlling skin stem-cell self-renewal is found](#)

Management Guide to Ecosystem Restoration Treatments:

Whitebark Pine Forests of the Northern Rocky Mountains, U.S.A.

Robert E. Keane
Russell A. Parsons



United States Department of Agriculture
Forest Service
Rocky Mountain Research Station
General Technical Report RMRS-GTR-232
January 2010



Keane, Robert E.; Parsons, Russell A. 2010. **Management guide to ecosystem restoration treatments: Whitebark pine forests of the northern Rocky Mountains, U.S.A.** Gen. Tech. Rep. RMRS-GTR-232. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 133 p.

ABSTRACT

Whitebark pine is declining across much of its range in North America because of the combined effects of mountain pine beetle epidemics, fire exclusion policies, and widespread exotic blister rust infections. This management guide summarizes the extensive data collected at whitebark pine treatment sites for three periods: (1) pre-treatment, (2) 1 year post-treatment, and (3) 5 years post-treatment (one site has a 10 year post-treatment measurement). Study results are organized here so that managers can identify possible effects of a treatment at their own site by matching it to the most similar treatment unit in this study, based on vegetation conditions, fire regime, and geographical area. This guide is based on the Restoring Whitebark Pine Ecosystems study, which was initiated in 1993 to investigate the effects of various restoration treatments on tree mortality, regeneration, and vascular plant response on five sites in the northern Rocky Mountains. The objective was to enhance whitebark pine regeneration and cone production using treatments that emulate the native fire regime. Since data summaries are for individual treatment units, there are no analyses of differences across treatment units or across sites.

Keywords: whitebark pine, ecosystem restoration, prescribed burning, fuel sampling, fire regime



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Discussion

Nearly all high and moderate intensity prescribed fire treatments combined with a cutting treatment effectively created desirable nutcracker caching habitat, as evidenced by the abundant nutcracker caching observed at nearly all sites. However, the whitebark pine regeneration that was expected to result from this caching has not yet materialized. Nearly all sites contain very few or no whitebark pine seedlings. This could be a result of many factors. First, we believe that many of the cached seeds have been reclaimed by the nutcrackers. We also feel that high rust mortality has reduced populations of cone-producing whitebark pine at or near our study areas so few seeds were actually available to be cached. At low levels of seed production, most seeds are consumed by the nutcrackers rather than forgotten and allowed to germinate. Next, severe site conditions could have killed many emerging seedlings. Our steep, high-mountain study sites experience deep snowpack, especially the Beaver Ridge site, which had more than 50 ft of snow in 1997. This heavy snowpack can "creep" down the slope and pull seedlings out of the ground. Moreover, most soils on our study site are highly erosive and spring snowmelts scoured the topsoil and washed away those seedlings rooted in it, especially in recently burned sites. Some researchers have identified a lag period of up to 40 years for the disturbed site to stabilize enough to allow whitebark pine to become established in upper subalpine zones (Agee and Smith 1984; Arno and Hoff 1990). Therefore, we believe that a 5-year evaluation period is too short to determine whitebark pine regeneration dynamics in these severe sites and a 10- or 20-year measurement might more accurately describe the success of our treatments. We recommend that sites where whitebark pine mortality is above 20 percent and rust infection is above 50 percent be planted with rust-resistant seedlings to shorten this long lag between disturbance and regeneration.

We lost many control plots on three study sites to wildfires. The fires that swept through the Bitterroot National Forest in 2000 burned the entire Coyote Meadows study site rendering all 30 control plots ineffective. The 2001 Dry Fork fire on the Salmon-Challis National Forest consumed 3 of 10 control plots on the Blackbird Mountain site. Embers from the prescribed burn at Blackbird Mountain started small fires in four of the control plots. The 2006 Gash Creek fire burned 5 of 10 control plots on the Smith Creek site and part of the Bear Overlook site (no control plots were burned). While a small wildfire at the Beaver Ridge site missed the control plots, it burned two cutting-only treatment units (3A and 2A; fig. 2e). The lack of sufficient control measurements makes it difficult to determine if changes measured on some of the treatment units were a result of the treatment and not of external factors such as climate. However, we found no significant difference in control plots for those sites that remained unburned (Keane and Parsons, in press).

Because of their lack of experience in burning high-elevation ecosystems, fire crews implemented prescribed burns under moister than desired conditions, thereby achieving less than desired fire intensity and severity. None of the fire crews had ever burned in the upper subalpine zone, so few wanted to risk burning in the desired dry conditions when the possibility of fire escape is high. In hindsight, as fire crews became familiar with burning in this high-elevation system, nearly all crews recognized that they could have easily achieved the higher severities. This may mean multiple treatments are needed to successfully realize burn plan objectives when experience is low or the consequences of escaped prescribed fires are severe.

Most treatments increased fuel loadings on most sites, especially the coarse woody debris (logs greater than 3 inches diameter). This was primarily because the prescribed fire burned through the bases of the abundant rust-killed whitebark pine snags within the treated stands. The newly fallen logs posed a low fuel hazard because they lacked fine fuels that contribute to increased fire spread. Their presence might actually improve the potential for whitebark pine regeneration by

the restoration treatment could also be a fuel reduction treatment.

Planting whitebark pine seedlings on the Beaver Ridge site was marginally effective in this study (approximately 30 percent survival after 5 years) because nursery techniques and planting guidelines for whitebark pine at the time of planting were not as refined as they are today (McCaughey and others 2009). Our seedlings were small and they were planted in mid-summer, just after snowmelt, so they had to survive three hot, dry months of drought. There is now extensive reference material for growing whitebark pine in nurseries and recommendations for planting whitebark pine (Scott and McCaughey 2006; McCaughey and others 2009; Izlar 2007). Our success would have been improved using today's technology. Planting should be done in mid-autumn and seedlings should be planted near structures, such as stumps, logs, and rocks, that provide stability from snowpack damage. Recently, Perkins (2004) found that grouse whortleberry had a positive effect and elk sedge had a negative effect on the growth and survival of planted whitebark pine seedlings. But Izlar (2007) found safe sites are more important to survival than sufficient whortleberry cover.

We recommend a fuel enhancement cutting implemented at least 1 year prior to a prescribed burn to ensure that burn objectives are fully realized. Adding cured slash to discontinuous fuelbeds facilitates burn effectiveness by providing additional fine fuel to aid fire spread into all areas of the treated stand and augment quick-drying fine fuel levels so the burn can be implemented in moister conditions. Prescribed burns had greater coverages (50 percent increase in burn coverage) and severities in fuel-enhanced stands. Fuel enhancement is an easy, inexpensive, and relatively rapid treatment that can be implemented by timber crews, fire crews, or contractors. We found that shrub and herbaceous fuels were much drier after the first hard frost in late summer or early autumn. Frost kills the aboveground foliage that allows the plants to take water from the soil so the aboveground plant structure can dry sufficiently for burning.

Ignition methods were important in this study. Most prescribed fires were ignited using strip head fires whose width was increased if higher fire intensities were desired. However, some study sites were so moist at ignition that even wide strips couldn't generate our desired intensities. Using the terra-torch and heli-torch, we were able to burn large areas to achieve the high target intensities. However, because these techniques may not always be available, the drip-torch is the primary ignition technique. To be effective, these drip-torch ignitions should be done in dry conditions to generate sufficient intensities to kill undesirable tree species. If possible, multiple burns may also produce similar effects as one high intensity fire.

Summary and Conclusions

Whitebark pine will continue to decline across its range as extensive exotic blister rust infections, more frequent and severe mountain pine beetle epidemics, and fire exclusion-oriented management policies continue. An extensive and long-term, integrated research and management program is needed to maintain this valuable tree species on the high-mountain landscape in the western United States and Canada. Restoration of this precious ecosystem will depend on cost-effective, coordinated efforts to

- conduct fundamental ecological research in whitebark ecosystems,
- develop methods to harvest seed from rust-resistant trees,
- refine nursery techniques to produce high quality, inexpensive rust-resistant seedlings for planting,

- create effective guidelines for planting rust-resistant seedlings and seeds,
- develop methods to plan and prioritize those areas in greatest need of whitebark pine restoration, and
- develop innovative prescribed burning and silvicultural cutting methods for restoring the keystone whitebark pine ecosystem (Keane and others, in press).

This management guide is a first step to develop restorative burning and cutting methods. Details in this report can be used to prioritize, plan, and implement restoration treatments in declining whitebark pine stands by providing a reference for determining effects of various prescribed burning and cutting treatments. Though we have not yet observed significant whitebark pine regeneration in many of our treated areas, we feel these techniques can be combined with planting of rust-resistant seedlings to effectively return whitebark pine to the landscape.

We recognize it will be impossible to implement the treatments explored in this study on all whitebark pine lands during this period of rapid decline. But, there will be critical whitebark pine forests that will require immediate and extensive proactive restoration, and the findings of this study will provide critical information for the successful planning and implementation of restoration activities. Since most whitebark pine forests are in protected areas such as National Parks, Wilderness Areas, and proposed Wilderness Areas that prohibit many of the treatments detailed in this report (Keane 2000), we feel wildland fire use (in essence, letting lightning-ignited fires burn under allowable parameters) will be the primary vehicle for treating deteriorating whitebark pine stands. No matter the treatment type, it will be critical to extensively monitor the effects of all direct (used in this study) and indirect (wildland fire use) treatments so we can refine and modify treatment guidelines in the future to account for local conditions and changing environments (for example, climate change and rust epidemics). Though the outlook may seem bleak for whitebark pine, recent exciting advances in research and many management successes will hopefully help secure the conservation of this keystone species.

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Effective actions for managing resilient high elevation five-needle white pine forests in western North America at multiple scales under changing climates

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ABSTRACT

Many ecologically important high elevation five-needle white pine (HEFNP) forests that historically dominated upper subalpine landscapes of western North America are now being impacted by mountain pine beetle (*Dendroctonus* spp.) outbreaks, the exotic disease white pine blister rust (*Cronartium ribicola*), and altered fire regimes. And more recently, predicted changes in climate may reduce HEFNP habitat and exacerbate adverse impacts of fire, beetles and rust. Management intervention using specially designed tactics implemented at multiple scales (range-wide, landscape, stand, and tree levels) are needed to conserve these keystone tree species. A goal of this intervention is to promote self-sustaining HEFNP ecosystems that have both resilience to disturbances and genetic resistance to white pine blister rust in the face of climate change. Many tools and methods are available for land managers, and in this paper, we summarize possible multi-scaled actions that might be taken as steps toward restoration of these valuable HEFNP forests. Long-term programs, such as inventory, mapping, planning, seed collection, seedling production, education, and research provide the materials for effective restoration at finer scales. Stand- and landscape-level passive and active treatments, such as silvicultural cuttings and prescribed fires in both healthy and declining forests, are described in detail and grouped by objectives, methods, and tactics. And last, there are critical pro-active tree-level actions of planting and protection that may be used alone or together to enhance success of other restoration actions. Administrative, policy, legislative, and societal barriers to implementation of an effective restoration effort are also discussed.

1. Introduction

It is now evident that many high elevation five-needle pine (HEFNP) forests in western North America are declining because of complex interactions across multiple disturbance factors (Keane et al., 2011) (Fig. 1). Forests consisting of two of the most widespread HEFNPs, whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*), are rapidly declining primarily due to the exotic disease white pine blister rust (WPBR) (*Cronartium ribicola*), but also recent frequent outbreaks of the native mountain pine beetle (MPB) (*Dendroctonus ponderosae*) (Tomback and Achuff, 2010; USFWS, 2018). Furthermore, the exclusion of wildland fire in these ecosystems over the last 100 years through fire suppression has resulted in greater surface and canopy fuel loadings and

successional replacement of some HEFNPs with more shade tolerant conifers (Keane, 2001). Climate change, however, has the potential to exacerbate WPBR and MPB outbreaks, increase wildfires above historical levels, and reduce suitable HEFNP habitat (Kotze, 1999; Kendall and Keane, 2001b; Keane et al., 2012; Smith-McKenna et al., 2014; Dudley et al., 2020). Forests of the other HEFNPs – foxtail pine (*P. balfouriana*), Great Basin bristlecone pine (*P. longaeva*), southwestern white pine (*P. strobiformis*), and Rocky Mountain (RM) bristlecone pine (*P. aristata*) – have yet to experience the major declines observed in limber and whitebark pine forests, but all are also in imminent danger from WPBR, and some from MPB mortality under climate change (Keane and Schoettle, 2011). Upper subalpine and treeline HEFNP forests cover a great portion of the western North American landscape (Arno and

Abbreviations: HEFNP, High Elevation Five Needle Pines; MPB, Mountain Pine Beetle; WPBR, White Pine Blister Rust; HRV, Historical Range of Variability; RAD, Resist, Accept, Direct climate mitigation strategy; RM, Rocky Mountain.

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Schwilk, 2009; Leirfallom et al., 2015; Stevens-Rumann et al., 2018).

3.2. Mapping

Mapping distributions of HEFNP species, threats to these species, spatial management context (e.g., land ownership, wilderness, and roads), forest structure, and stand condition (i.e., mortality and its causes) at multiple scales is an important first step towards planning effective restoration (Aubry et al., 2008b; Burns et al., 2008; Keane et al., 2012). Standard GIS spatial analysis techniques (Brown et al., 1994) can be used with available digital maps representing HEFNP ecology and management issues to provide the critical spatial information needed for many restoration efforts (see Keane et al. (2012) and Jenkins et al. in preparation, this issue). For example, gene conservation and seed collection guidelines can be geographically stratified by species distribution, biophysical settings, and ecological conditions following specified guidelines (e.g., see (Aubry et al., 2008b; Schoettle and Coop, 2017; Schoettle et al., 2019a)). Risk maps of WPBR infection levels may be useful to identify areas to monitor, collect seeds, and assess for intervention prioritization (Schoettle et al., 2019a) (Jenkins et al., in preparation, this issue). Effective mapping of HEFNP ranges and resources is best done at coarse spatial scales. Future HEFNP habitat layers have been modeled by several projects using empirical species distribution modeling approaches (Iverson and Prasad, 1998; Rehfeldt et al., 2006; McKenney et al., 2007), but this statistical approach has many limitations (Keane et al., 2020b).

3.3. Planning

The success of HEFNP restoration attempts will be greatly enhanced if a coordinated strategy can be developed that integrates the latest scientific findings into a comprehensive plan for species conservation across multiple scales of time, space, and organization. Because over 88% of whitebark pine forests (USFWS, 2020), and most other HEFNP forests, exist on public lands managed by state, provincial and federal agencies in the U.S. and Canada (Keane, 2000; Tomback and Achuff, 2010), government land management agencies play key roles in ensuring the survival of these ecologically valuable tree species. It is important that these government agencies employ a coordinated plan for species restoration to ensure that there are few conflicting actions that could result in further declines of HEFNP.

An inter-agency, trans-boundary restoration strategy for whitebark pine was crafted by Keane et al. (2012) to emphasize infrastructure, expertise, and agency strengths for implementation, and to make efficient use of scarce resources. This integrated strategy was then augmented with another report that accounted for climate change impacts on restoration strategies (Keane et al., 2017a). Together these provide guidance for planning successful, cost-effective actions for restoring declining whitebark pine forests. This effort is complemented by the National Whitebark Pine Restoration Plan, currently in development, which emphasizes priority areas for restoration work within units managed by different federal agencies (Tomback and Sprague, in preparation, this issue). Numerous regional or agency-based management guides and strategies have also been written to facilitate restoration of declining HEFNP ecosystems, especially whitebark pine forests. Regional developed strategies include the BLM whitebark pine strategy (Perkins et al., 2016), the Greater Yellowstone Ecosystem (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee, 2011), limber pine forests of the US Southern Rockies (Schoettle et al., 2019a), and whitebark pine forests of the Pacific Northwest (Aubry et al., 2008a). At local scales are the Crater Lake National Park (Beck and Holm, 2013), Greater Rocky Mountain National Park Area (limber pine) (Schoettle et al., 2019a), and Glacier National Park (Peterson, 1999). The Crown of the Continent (CCE) Pilot restoration strategy for whitebark pine is an ambitious multi-jurisdictional, transboundary plan that includes both whitebark and limber pine on US and Canadian lands

(Jenkins et al., in preparation, this issue). The CCE strategy and Keane et al. (2017a) efforts directly incorporate climate change impacts into the planning process, which is critically needed to be addressed in future planning documents.

An important step towards effective active restoration planning is to identify those areas that, with the proper management, have the greatest likelihood of success to support sustainable HEFNP populations and provide ecosystem services at the stand, landscapes, and regional levels under future climate change (Keane et al., 2012, 2017a). Even in regions where HEFNP mortality rates are comparatively low, such as the southern Rocky Mountains, the Sierra Nevada and interior Great Basin ranges, proactive prioritization strategies (see Schoettle and Sniezko (2007), Schoettle et al. (2019a)) may help prevent the severe declines experienced elsewhere. Prioritizing landscapes for restoration require assessments of those factors that have caused the decline of high elevation pines and those factors that could restrict or facilitate restoration activities, most importantly climate change. Assessments performed at this scale may be for several purposes: (1) to determine overall health and condition of the landscape or stand, (2) to inform design of restoration treatments, (3) to provide a context for assessing restoration goals (land ownership, accessibility for example), (4) to identify issues that could restrict or facilitate restoration efforts (e.g., grizzly bears, remote locations, wilderness), (5) to explain disturbance regimes that can be used to guide restoration design, (6) to locate areas that provide critical ecosystem services (watershed protection, recreation) and (7) to determine those areas that might support HEFNP forests under climate change. Collectively, these factors and others can be used to rank areas for restoration priority.

3.4. Conserving genetic diversity

Tree mortality from WPBR and MPB reduce both genetic diversity and population size of the HEFNP hosts. WPBR kills all age classes of HEFNP, including mature trees, but MPB especially targets larger-diameter individuals, which are cone-bearing (e.g., McDonald (1992)). Both threats reduce effective population size in HEFNPs and potentially create isolated groups and individuals, leading to inbreeding (Tomback and Kendall, 2001; Bower and Aitken, 2007). Before these threats significantly impact a HEFNP population, there is opportunity to capture native species' genetic diversity for gene conservation (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011). Millar et al. (2007) mentioned retaining of genetic diversity as an important action to enhance resilience to allow forests to respond to new disturbance regimes; prioritizing seed collections from only fast-growing trees may be counter-indicated in tomorrow's forests. Collections of seeds are the primary means to assess and conserve genetic diversity; gene conservation has been supported by the U.S. Forest Service (see Tomback et al., 2021, this issue). Seed collections, for example, began in 2001 for RM bristlecone pine and in 2003 for limber pine in the Southern Rocky Mountains (Schoettle, 2004). Extensive seed collections are being made before the occurrence of high mortality caused by MPB, WPBR, or wildland fire, enabling research on adaptive traits, genetic structure, and rust resistance screening to proceed. Range-wide Rocky Mountain bristlecone pine collections, accompanied by stand condition plot information for each sampling location, have been completed (Schoettle and Coop, 2017). Comparison of whitebark pine growth characteristics over geographic areas or large-scale common garden studies for whitebark pine indicate geographic variation in adaptive traits, particularly those related to climate (Bower and Aitken, 2006; Mahalovich et al., 2006).

Healthy ecosystems provide opportunities to gain information on the genetic structure of the pine host and population vulnerabilities to WPBR and other novel stresses, such as climate change (Schoettle et al., 2011; Schoettle et al., 2012). Seed zones in the U.S. were established for whitebark pine and limber pine (Mahalovich, 2006), and zones are being defined for RM bristlecone pine to aid in defining seed transfer

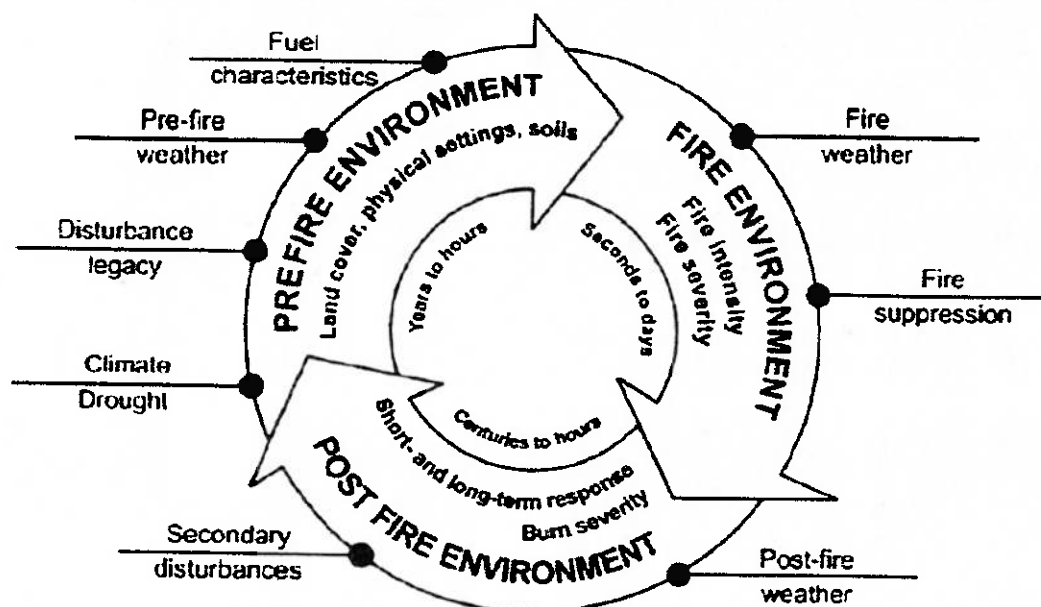


Fig. 3. The continuum of fire management. In this paper, wildfire management is stratified by actions that occur before the wildfire burns (pre-fire environment), during the fire (fire environment), and after the fire has occurred (post-fire environment) (from Graham et al. (2004)).

Keane et al., 2019). These management actions attempt to reduce wildland fuels to lessen wildfire severities (i.e., fuel treatment), but should also be designed to enhance resilience by (1) protecting fire-adapted species from unwanted damage or mortality; (2) improving tree vigor to facilitate survival after wildfires and other disturbances, and (3) enhancing regeneration by opening the stand to those tree species that can survive wildfire. There are generally three options for wildfire management while the wildfire is burning on HEFNP landscapes (fire environment, Fig. 3): (1) full suppression (FS), (2) partial suppression (PS), and (3) allowing wildfires to burn under an acceptable set of conditions (WFU; wildland fire use). Suppression tactics are best used to protect valuable elements of HEFNP ecosystems (detailed in Keane (2018)), but the consequences of suppression are usually greater fuel buildups, thereby increasing future wildfire severities. Perhaps the most effective restoration tool at the landscape level is managed wildfires or WFU (Black, 2004). WFUs are lightning-started fires that are allowed to burn under acceptable weather and site conditions specified in a local fire plan (Tanner, 1992). Aggressive use of WFU has the potential to be an efficient, economical, and ecologically viable method of restoring HEFNP forests in many areas, especially in wilderness areas (Keane et al., 2012). Landscapes where WFU might be contra-indicated are those with few HEFNP seed sources (e.g., high MPB and WPBR mortality) and where planting might be difficult.

6. Stand restoration treatments

The Keane et al. (2012, 2017a) range-wide whitebark pine strategies emphasized the need to create stand conditions that encourage natural regeneration (if WPBR resistance is high), conserve seed sources, promote rust resistance, and create resilient forests under changing climates. Objectives for most treatments, especially under changing climates (Keane et al., 2017a), include facilitating natural regeneration and planting rust-resistant seedlings, increasing HEFNP tree vigor, and reducing disturbance impacts. This can be accomplished by creating nutcracker caching habitat, reducing competing vegetation, decreasing surface and canopy fuels, manipulating forest structure and composition, and diversifying age class structure (Prichard et al., Millar et al., 2007). These actions can be implemented using a host of passive and active management actions to create areas where vigorous HEFNP trees can prosper in the face of climate change and impending disturbance

regimes (Swanston and Janowiak, 2012). In general, this usually involves some combination of locally designed silvicultural cuttings, prescribed burning, and planting rust-resistant seedlings. Any restoration action should also improve landscape heterogeneity while also facilitating HEFNP resilience, rust resistance, and sustainable cone crops (Keane et al., 2017a; Ireland et al., 2018). Stand-level treatment should be designed to address multiple objectives at landscape scales. Fuel reduction treatments, for example, should reduce competition and allow for natural and artificial pine regeneration, while also reducing fire hazard and risk (Prichard et al., 2021).

Mechanical cuttings include treatments that manipulate whitebark pine stand structure and composition, often by using chainsaws, to remove competing shade-tolerant, fire-sensitive tree species, such as subalpine fir, spruce, and mountain hemlock (example in Fig. 4). Traditional silvicultural approaches may have limited effectiveness in these high mountain stands because of the severity of the sites, unique ecology of HEFNPs, diverse disturbance regimes, and bird-mediated seed dispersal of some of the HEFNPs (Keane et al., 2017a). Silvicultural strategies must be specifically tailored to individual stands to address restoration concerns in high elevation pine forests (Waring and O'Hara, 2005). Six types of mechanical cuttings are currently being used in restoration treatments for whitebark pine. Keane and Parsons (2010b) created *nutcracker openings*, areas within which all trees except whitebark pine were cut, in successional advanced subalpine fir stands containing both healthy and dying WPBR-infected whitebark pine (Fig. 5). Nutcracker openings can also mimic patchy, mixed severity wildfires. Other cutting treatments include *group selection cuts* where all trees except whitebark pine are felled, and *thinnings* where all non-whitebark pine trees below a threshold diameter are cut (Chew, 1990; Eggers, 1990). *Girdling* subalpine fir trees has also been used to reduce whitebark pine competition because it is a fast, cost-effective means of *killing* competing subalpine fir (Jenkins, 2005), but the lowest live branches must be cut and the girdled trees are fuel that could foster future high severity wildfires that could kill those pine trees being restored. *Daylighting* (cutting of shade-tolerant competing species in a circle around whitebark pine trees) has been gaining favor among managers because it is cheap and easy, but there is little research on its effectiveness (see Fig. 4). One last cutting is *fuel enhancement* where subalpine fir trees are directionally felled to increase fuel loadings to better spread the fire (Keane and Arno, 2001). Keane and Parsons



Fig. 4. Mechanical cutting in whitebark pine treatment area. This person is performing a mechanical removal of trees around a whitebark pine, also called a “daylighting” treatment.

(2010b) found this treatment highly effective for widening of prescribed burning windows (lengthen flammability of fuelbed). In any mechanical treatment, it is important that slash be removed from treated sites to (1) allow nutcrackers full access to the ground for caching (Keane and Parsons, 2010b), (2) reduce potential pine mortality from *Ips* spp. beetles (Baker and Six, 2001), and (3) reduce severity of future unplanned future wildfires (Keane, 2018).

Prescribed burning may be the most ecologically desirable treatment because it best emulates wildland fire (Fig. 5), but it is also the most difficult and riskiest to implement (Keane et al., 2020a). Prescribed burns can be implemented at three intensities to mimic the three types of fire regimes common in HEFNP's forests: non-lethal surface fires, mixed severity burns, and stand-replacement fires (Murray et al., 1995a; Brown and Schoettle, 2008; Coop and Schoettle, 2016). The primary objectives of low intensity prescribed fires are to kill competing overstory and understory, to preserve the HEFNP component, and prepare the site for natural regeneration or planting (Keane, 2018). Moderate intensity prescribed burns mimic mixed severity fires where patches of variable size are burned depending on wind, canopy contagion, and fuel moisture conditions. A high intensity prescribed burn creates burned patches that are so large that seeds from competitors are unable to disperse into the center of the burn, allowing HEFNP regeneration decades of competition-free growth after germinated seeds are cached by nutcrackers. Mechanical cuttings and prescribed burns can be used together or separately to accomplish treatment objectives. Many populations of HEFNP's may be highly susceptible to fire mortality and prescribed burning may not be an option (Keane et al., 2020a). Research is needed to evaluate effective prescribed burning ignition patterns (Hiers et al., 2020), desirable ranges of wind, moisture and weather conditions (Keane and Parsons, 2010b), effective fuel loads to facilitate desired fire effects (Keane et al., 2020a).

6.1. Tree competition removal

Eliminating vegetation that competes with HEFNP trees is needed to improve tree vigor, which is increasingly important as the climate warms because it promotes resilience (Keane et al., 2017a; Retzlaff et al., 2018). Improved vigor often results in greater forest resilience because the trees have more resources to allocate to defenses against increasing

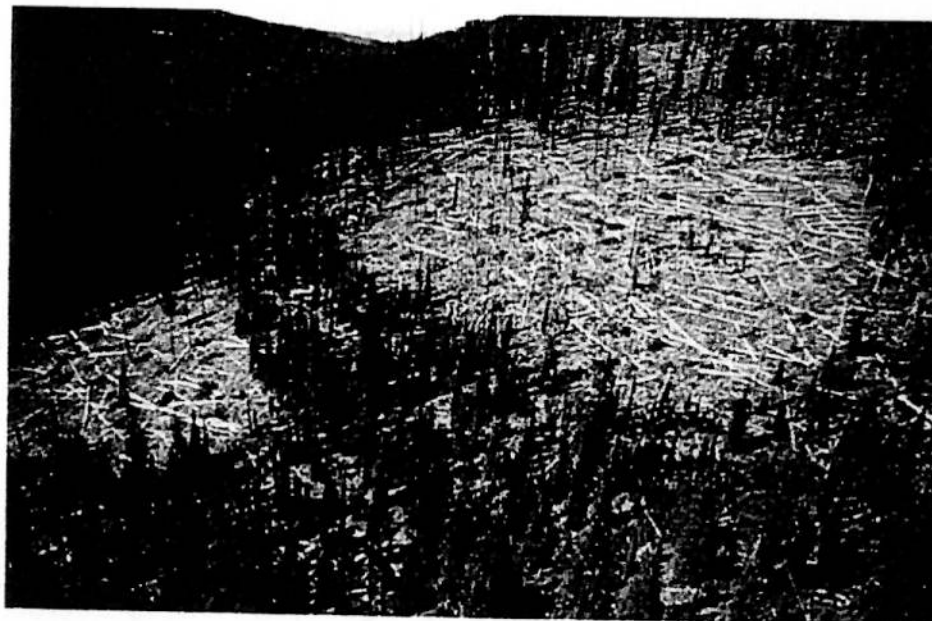


Fig. 5. A view of a “nutcracker opening” in the Keane and Parsons (2010b) restoration study that was implemented at the stand level and planned at the landscape level. In a nutcracker opening, all non-whitebark pine trees are cut and left on site. Slash is piled and burned. The openings were planted with rust-resistant seedlings three years later.



Fig. 6. Prescribed burning in the same landscape shown in Fig. 5. The objective of the prescribed fire was to kill all subalpine fir and Engelmann spruce, but leave whitebark pine mature trees alive. Auxiliary objectives were fuel reduction and seedling site preparation.

disturbance events (Churchill et al., 2013). Improved vigor may also increase the abundance of cone crops because trees may allocate more resources to reproduction (Morgan and Bunting, 1991). Increased vigor will also contribute to longevity and allow trees to remain on the landscape longer.

Mechanical thinning is the primary tool used for competition removal treatments (Keane and Arno, 2001). It is important that all competing shade-tolerant conifers be cut, including unwanted regeneration. However, this is rarely done because of the cost. Any residual trees of competing species, even small fir seedlings, will compromise efficacy of mechanical treatments, especially when future climate-mediated increases in productivity may accelerate successional advancement (Joyner, 1995; Fei et al., 2017; Gustafson et al., 2017). Therefore mechanical treatments may be enhanced by prescribed burning because, hopefully, fire will tend to kill most of the small and large shade-tolerant tree competitors and leave the more fire-tolerant whitebark pine individuals (Keane and Parsons, 2010a).

6.2. Wildland fuel reduction

Fuel treatments will undoubtedly play an important role in reducing future wildfire impacts on living rust-resistant HEFNP trees, and should therefore, be considered a viable restoration action (Rehfeldt and Jaquish, 2010; Spittlehouse and Stewart, 2004). Fuel treatments involve reducing canopy fuels by cutting, masticating, or burning living subalpine fir, spruce, and other shade-tolerant conifer trees and reducing surface fuels by burning, cutting, or piling. Reducing fuels in or near stands that contain valuable rust-resistant trees may be an important hedge against losing them to future wildfires. Fuel treatments can also be designed in the context of HEFNP restoration treatments, and vice versa, with any reduction of canopy and surface fuels considered a secondary objective. Many contemporary fuel treatments, such as mastication, canopy thinning, and chipping, are rarely designed with ecological relationships in mind. There is also some risk that live HEFNP trees could be cut during fuel reduction treatments. And conversely, restoration treatments that do not also reduce fuels may result in

unnecessary losses of seed sources from future wildfires.

7. Tree level actions

7.1. Planting

As HEFNP forests continue to decline, there will be fewer seeds produced and thus fewer available for pine regeneration (Keane and Parsons, 2010b). For example, in whitebark pine stands with high WPBR and MPB mortality, the low number of cones produced by surviving trees are highly sought after by pre-dispersal seed predators—especially pine squirrels, which may take unripe cones, but also nutcrackers—leaving few seeds to ripen and be available for nutcracker caching (McKinney and Tomback, 2007; McKinney et al., 2009). There also may be insufficient whitebark pine seed to naturally regenerate burned areas because of high nutcracker retrieval of caches (Keane and Parsons, 2010b; Tomback and Achuff, 2010). This same reasoning can also be applied to other HEFNP, and especially those pines that depend on Clark's nutcrackers for long distance seed dispersal (Tomback and Kendall, 2001; Tomback et al., 2011). Therefore, planting rust-resistant seedlings may be the only option to regenerate the species in large-scale high elevation burned areas (Howard, 1999; Hoff et al., 2001; Scott and McCaughey, 2006; Schoettle et al., 2019b). In addition, if local seed sources contain little or no heritable resistance to WPBR, artificial regeneration with rust-resistant seedlings may both increase population size and augment resistance into the future (Schoettle et al., 2019a). If high elevation landscapes have higher than 60% HEFNP mortality, it may be necessary to plant with putatively rust-resistant pine seedlings (Keane et al., 2012; Leirfallom et al., 2015).

Effective planting guidelines have been developed for whitebark pine (Scott and McCaughey, 2006; Izlar, 2007; McCaughey et al., 2009) and limber pine (Casper, 2015). The new guidelines have resulted in improvements in whitebark pine seedling survival (Izlar, 2007), but planting guidelines for the other HEFNPs are still needed. Appropriate microsites and shelter (i.e., nurse objects such as boulders, cobble, logs, and tree trunks) are important for successful establishment of both wind

2018

Forest structure provides the income for reproductive success in a southern population of Canada lynx

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Abstract. Understanding intrinsic and extrinsic drivers of reproductive success is central to advancing animal ecology and characterizing critical habitat. Unfortunately, much of the work examining drivers of reproductive success is biased toward particular groups of organisms (e.g., colonial birds, large herbivores, capital breeders). Long-lived mammalian carnivores that are of conservation concern, solitary, and territorial present an excellent situation to examine intrinsic and extrinsic drivers of reproductive success, yet they have received little attention. Here, we used a Canada lynx (*Lynx canadensis*) data set, from the southern periphery of their range, to determine if reproductive success in a solitary carnivore was consistent with capital or income breeding. We radio-marked and monitored 36 female Canada lynx for 98 lynx years. We evaluated how maternal characteristics and indices of food supply (via forest structure) in core areas influenced variation in body condition and reproductive success. We characterized body condition as mass/length and reproductive success as whether a female produced a litter of kittens for a given breeding season. Consistent with life-history theory, we documented a positive effect of maternal age on body condition and reproductive success. In contrast to predictions of capital breeding, we observed no effect of pre-pregnancy body condition on reproductive success in Canada lynx. However, we demonstrated statistical effects of forest structure on reproductive success in Canada lynx, consistent with predictions of income breeding. The forest characteristics that defined high success included (1) abundant and connected mature forest and (2) intermediate amounts of small-diameter regenerating forest. These attributes are consistent with providing abundant, temporally stable, and accessible prey resources (i.e., snowshoe hares; *Lepus americanus*) for lynx and reinforce the bottom-up mechanisms influencing Canada lynx populations. Collectively, our results suggest that lynx on the southern range periphery exhibit an income breeding strategy and that forest structure supplies the income important for successful reproduction. More broadly, our insights advance the understanding of carnivore ecology and serve as an important example on integrating long-term field studies with ecological theory to improve landscape management.

Key words: capital breeding; felids; habitat quality; habitat–fitness relationship; income breeding; *Lepus americanus*; *Lynx canadensis*; maternal effects; reproductive strategy; reproductive success.

INTRODUCTION

Individual reproductive success is an essential component of population dynamics, population persistence, as well as lifetime fitness (Stearns 1992). Therefore, ecologists and conservation biologists are keenly interested in evaluating the relative importance of intrinsic and extrinsic factors affecting reproductive success (Frederiksen et al. 2014). Intrinsic factors include many attributes such as cohort, genotype, maternal condition, or age, whereas extrinsic factors include climate, weather, population density, or the availability and distribution of food. Many of these factors exhibit spatial or temporal variation and thus provide opportunities to evaluate how their variation is linked to individual reproductive success (e.g., Clutton-Brock and

Sheldon 2010). Moreover, a central mechanism to the conservation of endangered and threatened species is the designation of critical habitat (e.g., U.S. Endangered Species Act and Canada Species at Risk Act), which requires an understanding of habitat quality through the characterization of habitat–fitness relationships (e.g., via reproductive success, survival, or both) despite the challenges of doing so (e.g., Van Horne 1983, Mosser et al. 2009). Indeed, the insights generated from assessing intrinsic and extrinsic drivers of individual reproductive success are vast for both ecological theory and policy-relevant decision making. Unfortunately, however, the current state of understanding on factors driving individual reproductive success is disproportionately influenced by the particular groups of organisms where long-term studies have been conducted (e.g. birds, social mammals, large herbivores, capital breeders; Hamel et al. 2010, Clutton-Brock and Sheldon 2010, Saether et al. 2013, Uboni et al. 2017).

Reproduction is constrained by trade-offs associated with resource acquisition and the allocation of those resources to

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TABLE 1. Description of forest structural classes within the Canada lynx (*Lynx canadensis*) study areas in northwestern Montana, USA.

Forest structure class	Stand description	Relationship to snowshoe hares
Open	No trees or canopy present, low horizontal cover.	Low density of snowshoe hares (Griffin and Mills 2009, Holbrook et al. 2017b)
Sparse forest	Naturally sparsely stocked or mechanically thinned stands with a discontinuous canopy and a visible forest floor, low horizontal cover.	Low density of snowshoe hares (Griffin and Mills 2009, Holbrook et al. 2017b)
Small-diameter regenerating forest	Regenerating forests generally due to forest management with smaller sized (~10–15 cm DBH) trees, intermediate canopy cover, and high horizontal cover.	Capable of producing high density of snowshoe hares over a limited time frame, but hares are potentially difficult to access and kill for lynx because of high stem densities (Griffin and Mills 2009, Lewis et al. 2011, Ivan et al. 2014, Cheng et al. 2015, Ivan and Shenk 2016, Holbrook et al. 2017b)
Medium-diameter regenerating forest	Regenerating forests from forest management with medium sized (~15–20 cm DBH) trees and continuous canopy and high horizontal cover.	Capable of producing high density of snowshoe hares over a limited time frame, but hares are somewhat accessible because of intermediate stem densities (Griffin and Mills 2009, Lewis et al. 2011, Ivan et al. 2014, Cheng et al. 2015, Ivan and Shenk 2016, Holbrook et al. 2017b)
Mature forest	A multistoried or uneven-aged stand with a median DBH of 26 cm (10 inches). This DBH is reflective of the multistoried nature of the structure class, but despite this DBH, there was a comparatively high proportion (i.e., 22%) of large trees (≥ 38 cm in DBH). Common attributes in this class were substantial understory (e.g., seedlings and saplings) and horizontal cover, continuous canopy, and no evidence of recent disturbance.	Capable of producing medium density of snowshoe hares over a long time frame, and kill rates are higher for lynx because stem densities are lower than regenerating classes (Griffin and Mills 2009, Squires et al. 2010, Ivan et al. 2014, Ivan and Shenk 2016)

Note: We characterized our predicted relationship between forest structure and snowshoe hare densities using literature from the Northern and Southern Rocky Mountains, USA.

abundance of forest structure types (McGarigal et al. 2012). We characterized landscape composition by simply calculating the percent composition of small- and medium-diameter regenerating forest in each female's core area (Table 2). Consistent with income breeding, we generally predicted body condition of female lynx would be unrelated to food resources. However, we expected reproductive success by lynx to be positively related to small- and medium-diameter regenerating forest because snowshoe hares (i.e., food resources) tend to reach the highest densities at intermediate structural stages (e.g., Ivan et al. 2014, Cheng et al. 2015).

A novel metric we used to characterize amount and configuration of mature forest patches was "area-normalized correlation length" (Table 2). Correlation length is a landscape metric based on the average extensiveness of connected patches of a focal habitat type within a given landscape (McGarigal et al. 2012). This can be interpreted as the average distance an animal could travel within each female's core area without leaving mature forest, starting from a random point and moving in a random direction. Because this metric is sensitive to area, we area-normalized the correlation length (S. Cushman and K. McGarigal, *personal communications*) by (1) quantifying the "potential" correlation length for each core area if the entire core area was one contiguous patch of mature forest; (2) quantifying "realized" correlation length for each core area, or the ability for the female to traverse her core area without exiting mature forest given the existing forest mosaic; (3) then dividing the "realized" by the "potential" for each core area. This resulted in a mature forest connectivity index (MFCI) scaled 0–1, with values closer to 0 representing low connectivity and values closer to 1 representing high connectivity. Similar

to the previous predictions consistent with income breeding, we expected body condition of female lynx to be unrelated to mature forest connectivity, but predicted reproductive success would be positively related with high connectivity of mature forest. Mature forest provides abundant, temporally consistent, and accessible snowshoe hares for Canada lynx in the Rocky Mountains (Table 1; Griffin and Mills 2009, Ivan et al. 2014, Holbrook et al. 2017b) and lynx are more successful at killing snowshoe hares in mature forest than regenerating forest (Ivan and Shenk 2016). In addition, lynx exhibit strong selection for mature forest and use this structural stage twice as much as any other during both winter and summer seasons (Holbrook et al. 2017a).

Statistical analyses

We used generalized linear mixed-models (GLMM; Bolker et al. 2009) to assess our predictions on income vs. capital breeding in Canada lynx (Fig. 1). We used a Gaussian and binomial distribution (with a logit link) for our analysis of body condition and reproductive success, respectively. We included the identity of individual females as a random effect to control for repeated measures of the same individual over time (Bolker et al. 2009). Initially, we assessed the effect of each covariate on body condition and reproductive success and determined if there was support for a curvilinear relationship based on the Akaike information criterion corrected for sample size (AIC_c; Burnham and Anderson 2002). For each assessment, we reported unstandardized regression coefficients (β), standard errors (SE), *P* values, and sample sizes (*n*). If multiple covariates were characterized as important based on Hosmer and Lemeshow (2000) criteria (e.g., $\alpha = 0.20$) and were uncorrelated

TABLE 2. Covariates used in evaluating the evidence for income and capital breeding by female Canada lynx (*Lynx canadensis*) in northwestern Montana, USA, during 1998–2012.

Covariates	Description
Maternal characteristics	
Body condition index	mass/length (kg/cm) from nose to the tip of tail
Age at parturition	three ordinal categories: 1 = 2 yr olds, 2 = 3 yr olds, and 3 = >3 yr old
Reproductive effort at $t - 1$	reproductive cost of producing a litter of kittens the previous year ($t - 1$); 0 = no litter at $t - 1$, 1 = litter of kittens at $t - 1$
Forest structure (index of food resources)	
Percentage of small-diameter regenerating forest	percentage of core area
Percentage of medium-diameter regenerating forest	percentage of core area
Mature forest	mature forest connectivity index (MFCI), which is an area normalized correlation length (index ranging from 0 to 1)

($|r| < 0.70$), we combined them into a multivariate model. If a multivariate model was constructed, we assessed the fit of the Gaussian model using Spearman's correlation coefficient (r_s) between predicted and observed values and used the area under the curve of a receiver operating characteristic for the binomial model (AUC of ROC; Hosmer and Lemeshow 2000). All statistical analyses were performed in program R (R Core Team 2013) using the following libraries: lme4 (Bates et al. 2014), effects (Fox 2003), and ROCR (Sing et al. 2005).

RESULTS

We monitored 36 females (Yaak = 17, Seeley = 19) of reproductive age (≥ 2 yr old) for an average of 2.7 ± 1.9 yr of observation per female (mean $\pm$ SD, range = 1–7 yr). This resulted in a total of 98 lynx years monitored over the study (1998–2012). Females produced 61 litters (150 kittens), which resulted in a raw parturition percentage of 62%. Mean female body mass was 9.04 kg (range = 7.25–11 kg) and the body condition index (mass/length) ranged from 0.20 to 0.31 with a mean of 0.24.

Composition of structure classes within female core areas was variable and ranged from relatively contiguous mature forest among a mixture of other forest structure types, to

those typified by smaller and more isolated mature forest patches surrounded by different forest structures (Fig. 4). Mature forest was the dominant forest structure type in core areas, comprising $49\% \pm 13\%$ (mean $\pm$ SD, range = 7–79%; see Appendix S2 for forest metrics associated with mature forest). Mature forest was multi-storied with a substantial understory and a dense canopy. For instance, tree sizes for mature forest were approximately distributed as follows: 2.0–12.7 cm DBH (11%), 12.7–25.4 cm DBH (37%), 25.4–38 cm DBH (30%), and >38–72 cm DBH (22%; Appendix S2). Medium-diameter regenerating forests comprised an average $24\% \pm 18\%$ (range 1–54%) and small-diameter regenerating forests comprised $13\% \pm 6\%$ (range = 1–26%) of core areas. Open and sparse forest structure types comprised the remaining area ($4\% \pm 4\%$, range 0–12%; $10\% \pm 7\%$, range 3–24%, respectively).

Body condition

Consistent with our predictions, only maternal age was related to changes in female body condition (Table 3). We observed a positive effect of age on body condition, with female lynx >3 yr old exhibiting better condition than 2-yr olds (Fig. 5). Neither reproductive effort at $t - 1$ nor indices of food resources (i.e., forest structure classes) were statistically related to variation in female body condition (Table 3). We did not develop a multivariate model because only female age was statistically related to body condition in our univariate analyses.

Reproductive success

Based on univariate analyses, reproductive success of female lynx was positively related to maternal age and the connectivity of mature forest (Table 3). However, reproductive success was negatively related to medium-diameter regenerating forests and exhibited a curvilinear relationship with small-diameter regenerating forest (Table 3). Neither body condition nor reproductive effort at $t - 1$ was statistically related to reproductive success of female lynx.

We developed a multivariate model characterizing reproductive success of female Canada lynx, which included a linear effect of maternal age, medium-diameter regenerating forest, and mature forest connectivity. Additionally, we included a curvilinear effect of small-diameter regenerating forest. Once combined, the effect of maternal age and

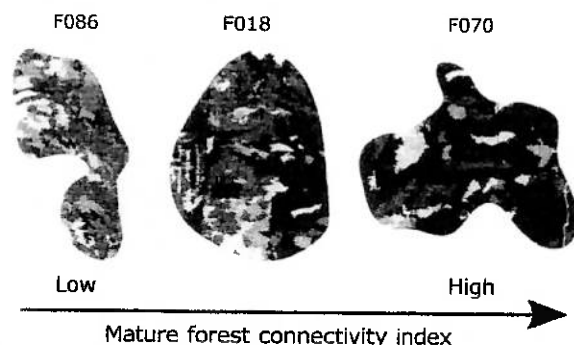


FIG. 4. Example core areas of female Canada lynx (*Lynx canadensis*) in the Yaak and Seeley study areas in northwestern Montana, USA. Core areas of females that produced litters had higher connectivity of mature forest (dark green) and ~12–20% composition of small-diameter regenerating forests (yellow). Forest structure categories include mature forest (dark green), medium-diameter regenerating forest (light green), small-diameter regenerating forest (yellow), sparse forest (orange), and open areas (red).

49
4
10
24
13
37
100

TABLE 3. Marginal coefficients from our GLMM univariate assessment of factors influencing variation in body condition and reproductive success of female Canada lynx (*Lynx canadensis*) in northwestern Montana, USA, during 1998–2012.

Covariates	β	SE	P	n	Females
Body condition					
Age	0.015	0.005	0.001	43	28
Reproductive effort at $t - 1$	0.001	0.012	0.948	24	15
Percentage of small-diameter regenerating forest	-0.001	0.001	0.335	44	22
Percentage of medium-diameter regenerating forest	0.000	0.001	0.451	44	22
Connectivity of mature forest	-0.006	0.018	0.732	44	22
Reproductive success					
Body condition	-18.227	16.381	0.266	52	30
Age	0.794	0.416	0.056	85	34
Reproductive effort at $t - 1$	0.456	0.989	0.645	61	23
Percentage of small-diameter regenerating forest	0.832	0.240	0.001	78	23
(Percentage of small-diameter regenerating forest) ²	-0.026	0.008	0.001	78	23
Percentage of medium-diameter regenerating forest	-0.076	0.038	0.042	78	23
Connectivity of mature forest	2.719	1.787	0.128	78	23

Notes: Unstandardized beta coefficients (β), standard errors (SE), P values, sample sizes (n), and number of females are identified. Univariate tests suggesting a statistical effect ($\alpha = 0.20$; Hosmer and Lemeshow 2000) are highlighted in boldface type.

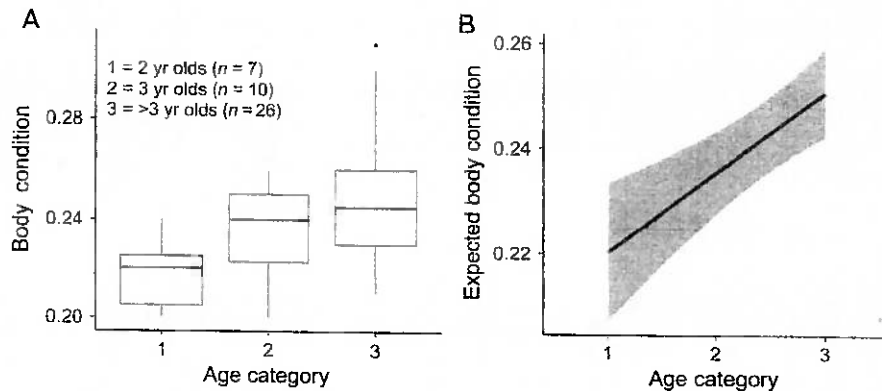


FIG. 5. (A) Box plot characterizing the positive relationship between body condition and maternal age for female Canada lynx (*Lynx canadensis*) northwestern Montana, USA. Middle line, median; box edges, interquartile range (IQR); whiskers, $\leq 1.5 \times$ IQR beyond the box. (B) Predicted relationship from our GLMM highlighting the marginal effect of maternal age on body condition. Gray bands indicate the 90% CIs.

medium-diameter regenerating forest became statistically insignificant ($P > 0.60$, $n = 68$ seasons, females = 22), while the effect of small-diameter regenerating forest and mature forest connectivity remained significant ($P = 0.002$ – 0.052 , $n = 68$ seasons, females = 22). The connectivity of mature forest and the amount of small-diameter regenerating forest were the most important covariates influencing reproductive success of female lynx. The AUC for our multivariate model indicated reasonable predictive performance (AUC = 0.85).

The probability of producing a litter was highest for females that had core-use areas with ~12–20% of small-diameter regenerating forest ($\beta_{\text{small-diameter}} = 1.57$, SE = 0.59; $\beta_{\text{small-diameter}^2} = -1.01$, SE = 0.33), and increased with increasing connectivity of mature forest ($\beta_{\text{MFCI}} = 1.45$, SE = 0.75; Fig. 6). The influence of small-diameter forests on female productivity was mediated by the connectivity of mature forest patches. In core areas with high connectivity of mature forest, the probability of producing a litter increased from 0.5 to 1.0 as the proportion of small-diameter regenerating forest increased from ~5% to ~10%. The probability of producing a litter remained consistently high

up to ~20% of small-diameter forest within core areas, and then declined slightly beyond ~20% (Fig. 6B, lower right quadrant). Conversely, in core areas with low connectivity of mature forest, the optimal was ~17% for small-diameter regenerating forest; however, the probability of producing a litter did not exceed 0.80 (Fig. 6B, upper left quadrant) emphasizing the importance of connected mature forest (i.e., lower right quadrant where probability of producing a litter reaches 1.0).

DISCUSSION

Consistent with our hypothesis, our analyses support the notion that Canada lynx on the southern range periphery exhibit a strategy of income breeding (Jönsson 1997, Houston et al. 2006). First, the main drivers of reproductive success for females were the combined effects of highly connected mature forest and intermediate amounts of small-diameter regenerating forest within core use areas (Fig. 6). The most likely mechanism associated with these findings was food limitation, which has been demonstrated in many



The Unseen Effects of Deforestation: Biophysical Effects on Climate

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Climate policy has thus far focused solely on carbon stocks and sequestration to evaluate the potential of forests to mitigate global warming. These factors are used to assess the impacts of different drivers of deforestation and forest degradation as well as alternative forest management. However, when forest cover, structure and composition change, shifts in biophysical processes (the water and energy balances) may enhance or diminish the climate effects of carbon released from forest aboveground biomass. The net climate impact of carbon effects and biophysical effects determines outcomes for forest and agricultural species as well as the humans who depend on them. Evaluating the net impact is complicated by the disparate spatio-temporal scales at which they operate. Here we review the biophysical mechanisms by which forests influence climate and synthesize recent work on the biophysical climate forcing of forests across latitudes. We then combine published data on the biophysical effects of deforestation on climate by latitude with a new analysis of the climate impact of the CO₂ in forest aboveground biomass by latitude to quantitatively assess how these processes combine to shape local and global climate. We find that tropical deforestation leads to strong net global warming as a result of both CO₂ and biophysical effects. From the tropics to a point between 30°N and 40°N, biophysical cooling by standing forests is both local and global, adding to the global cooling effect of CO₂ sequestered by forests. In the mid-latitudes up to 50°N, deforestation leads to modest net global warming as warming from released forest carbon outweighs a small opposing biophysical cooling. Beyond 50°N large scale deforestation leads to a net global cooling due to the dominance of biophysical processes (particularly increased albedo) over warming from CO₂ released. Locally at all latitudes, forest biophysical impacts far outweigh CO₂ effects, promoting local climate stability by reducing extreme temperatures in all seasons and times of day. The importance of forests for both global climate change mitigation and local adaptation by human and non-human species is not adequately captured by current carbon-centric metrics, particularly in the context of future climate warming.

Keywords: forest, biophysical effects, temperature, climate policy, deforestation/afforestation

deforestation and all emitted CO₂ would have had an effect in a given band, but the point of the analysis was to isolate the temperature change caused by forests in a given latitude. We determined the latitudinal sensitivity to warming in response to added CO₂ from a re-analysis of global 2 m temperature data (CERA-20C) obtained from the European Centre for Medium-Range Weather <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/cera-20c>. We compared average temperatures from 1901 to 1910 and 2001–2010, by latitude on land only (inadequate land only data for 50–60S and 80–90N; for those, we do not report a locally felt CO₂ effect). Then we divided the temperature change for each latitude band by the change in global temperature over the same period. We scaled the effect of CO₂ emitted by a given 10° latitude band by this sensitivity to represent the influence of non-linear responses such as polar amplification (see **Supplementary Information 1** and **Supplementary Table 2**).

RESULTS

Biophysical Effects of Deforestation on Local Climate: A Broader Context

Our analysis is the first to compare regional scale biophysical and CO₂ impacts from regional scale deforestation but the literature is replete with data on local biophysical impacts. The results for local biophysical effects (100s of m to 100s of km) agree with our results at the regional scale (below). **Figures 2, 3** synthesize local biophysically-driven temperature responses to deforestation, as indicated by forest/no-forest comparisons or forest change over time, from the scientific literature. Satellite and flux tower data indicate that surface temperatures in tropical forests are significantly lower than in cleared areas nearby. On an annual basis, local surface cooling of 0.2–2.4°C has been observed (mean 0.96°C, **Figure 2** and **Supplementary Information 2**). In the temperate zone, satellite studies of land surface temperature (which is more sensitive than the temperature of the air at 2 m) have shown biophysical cooling from forest cover, or biophysical warming from deforestation (0.02–1.0°C, mean of 0.4°C; see **Figure 2** and **Supplementary Information 2**). Both *in situ* and satellite data generally indicate an average annual cooling of under 1°C from boreal deforestation (**Figure 2**). Across latitudinal zones, warming from deforestation is generally greater during the day, and during the dry (hot) season (**Figure 3**).

CO₂-Induced Warming Versus Biophysical Effects on Regional (Local) Temperature From Deforestation by 10° Latitude Band

As expected, the regionally felt effect of regionally (10° band) produced CO₂ is very small compared to any individual biophysical effect or the sum of all non-CO₂ effects (**Figure 4**). These results indicate that the net impact of all non-CO₂ effects is negligible between 20 and 30N. Beyond 30N the local biophysical response to deforestation is cooling. In the broader literature,

this latitude of net zero biophysical effect on local temperature is generally between 30 and 40N (**Figure 1**).

Biophysical Effects on Global Temperature From Deforestation by 10° Latitude Band

For most latitudinal bands, the strongest biophysical effect of deforestation is cooling from albedo changes. In the tropics, however, the warming effect of lost roughness is comparable to or greater than the albedo effect (**Figure 5A**). Adding the warming from lost evapotranspiration, the net biophysical effect from tropical deforestation is global warming, as much as 0.1°C contributed each by latitudes 0°–10°S and 0°–10°N. The net biophysical effect of intact tropical forest, therefore, is global cooling; slightly more cooling if BVOCs are also considered (see **Figure 5B**). Roughness effects are generally greater than evapotranspiration effects across latitudes providing a strong counterbalance to albedo effects (Davin and de Noblet-Ducoudré, 2010; Burakowski et al., 2018; Winckler et al., 2019b; **Figure 5A**). Albedo almost balances the combined effect of roughness, evapotranspiration, BVOC and non-linear effects between 20 and 30°N resulting in close to zero net biophysical effect on global temperature (**Figure 5B**). From 30–40°N and northward, albedo dominates, and the net biophysical effect of deforestation is cooling.

CO₂-Induced Warming Versus Biophysical Effects on Global Temperature From Deforestation by 10° Latitude Band

From 30°S to 30°N, the biophysical effect of deforesting a given 10° latitudinal band is about half as great and in the same direction as the CO₂ effect: global warming. Biophysical warming is around 60% as great as warming from released CO₂ in the outer tropics (20°S–10°S and 10°N–20°N) and about 35% as great in the heart of the tropics (10°S–10°N). Biophysical cooling due to deforestation from 30°N to 40°N offsets about 40% of the warming associated with carbon loss from deforestation; from 40°N to 50°N biophysical effects offset 85% of CO₂ effects (**Figure 5B**). Above 50°N, biophysical global cooling is 3–6 times as great as CO₂ induced global warming. The net impact of deforestation (effects of CO₂, biophysical processes and BVOC combined) is warming at all latitudes up to 50N (**Figure 5C**). Thus, from 50S to 50N, an area that encompasses approximately 65% of global forests (FAO, 2020), deforestation results in global warming (**Figure 5C**).

DISCUSSION

All Forests Provide Local Climate Benefits Through Biophysical Effects

Ignoring biophysical effects on local climate means casting aside a powerful inducement to promote global climate goals and advance forest conservation: local self-interest. The

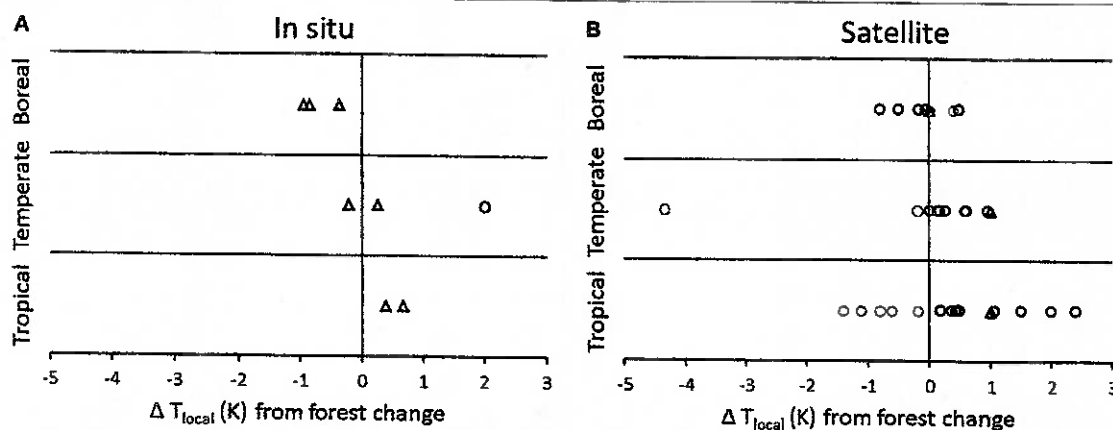


FIGURE 2 | Local average annual temperature change in response to deforestation (black symbols) or afforestation (green symbols) as determined by comparing neighboring forested and open land (space for time approach) or measuring forest change over time in the tropics, temperate and boreal zones, by (A) *in situ* or (B) satellite based land surface temperature measurements (0 m, triangles) or air temperature measurements (2 m, circles). See **Supplementary Information 2** for data sources.

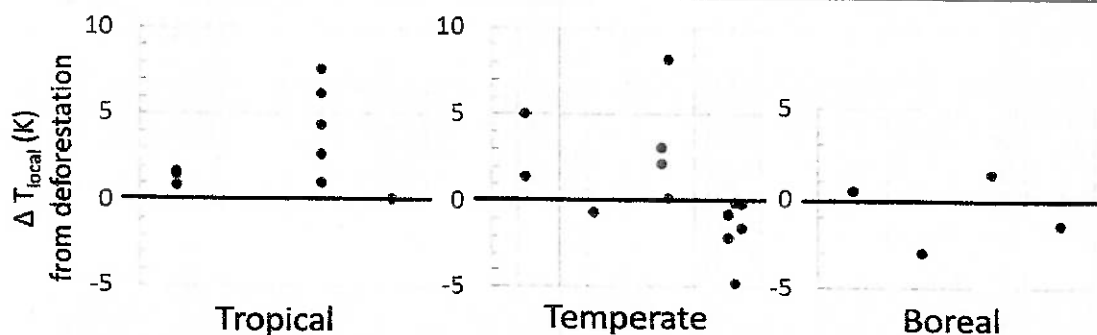


FIGURE 3 | Local temperature change in response to deforestation by season and time of day in the various climate zones as determined by comparing neighboring forested and open land (space for time approach) or measuring forest change over time. Warm/dry season response, averaged over the entire diurnal cycle, in red shading and cold/wet season response in blue shading. Daytime response, averaged over the entire annual cycle, in yellow shading and nighttime response in gray shading. See **Supplementary Information 3** for data sources.

biogeochemical effect of forests tends to dominate the biophysical effect at the global scale because physical effects in one region can cancel out effects in another. Nevertheless, biophysical effects are very important, and can be very large, at the local scale (e.g., Anderson-Teixeira et al., 2012; Bright et al., 2015; Jiao et al., 2017; **Figures 2–4**). The role of forests in maintaining critical habitat for biodiversity is well known, but new research on extinction confirms the role of forests in maintaining critical climates to support biodiversity. Changes in maximum temperature are driving extinction, not changes in average temperature (Román-Palacios and Wiens, 2020). Deforestation is associated with an increase in the maximum daily temperature throughout the year in the tropics and during the summer in higher latitudes (Lee et al., 2011; Zhang et al., 2014). Of course deforestation also increases average daytime temperatures in boreal, mid-latitude and tropical forests (**Figure 3**). The biophysical effects of forests also moderate local and regional temperature extremes such that extremely hot days are significantly more common following deforestation even in the mid- and high latitudes

(Vogel et al., 2017; Stoy, 2018). Historical deforestation explains ~1/3 of the present day increase in the intensity of the hottest days of the year at a given location (Lejeune et al., 2018). It has also increased the frequency and intensity of hot dry summers two to four fold (Findell et al., 2017). Local increases in extreme temperatures due to forest loss are of comparable magnitude to changes caused by 0.5°C of global warming (Seneviratne et al., 2018). Forests provide local cooling during the hottest times of the year anywhere on the planet, improving the resilience of cities, agriculture, and conservation areas. Forests are critical for adapting to a warmer world

Forests also minimize risks due to drought associated with heat extremes. Deep roots, high water use efficiency, and high surface roughness allow trees to continue transpiring during drought conditions and thus to dissipate heat and convey moisture to the atmosphere. In addition to this direct cooling, forest ET can influence cloud formation (Stoy, 2018), enhancing albedo and potentially promoting rainfall. The production of BVOCs and organic aerosols by forests accelerates with

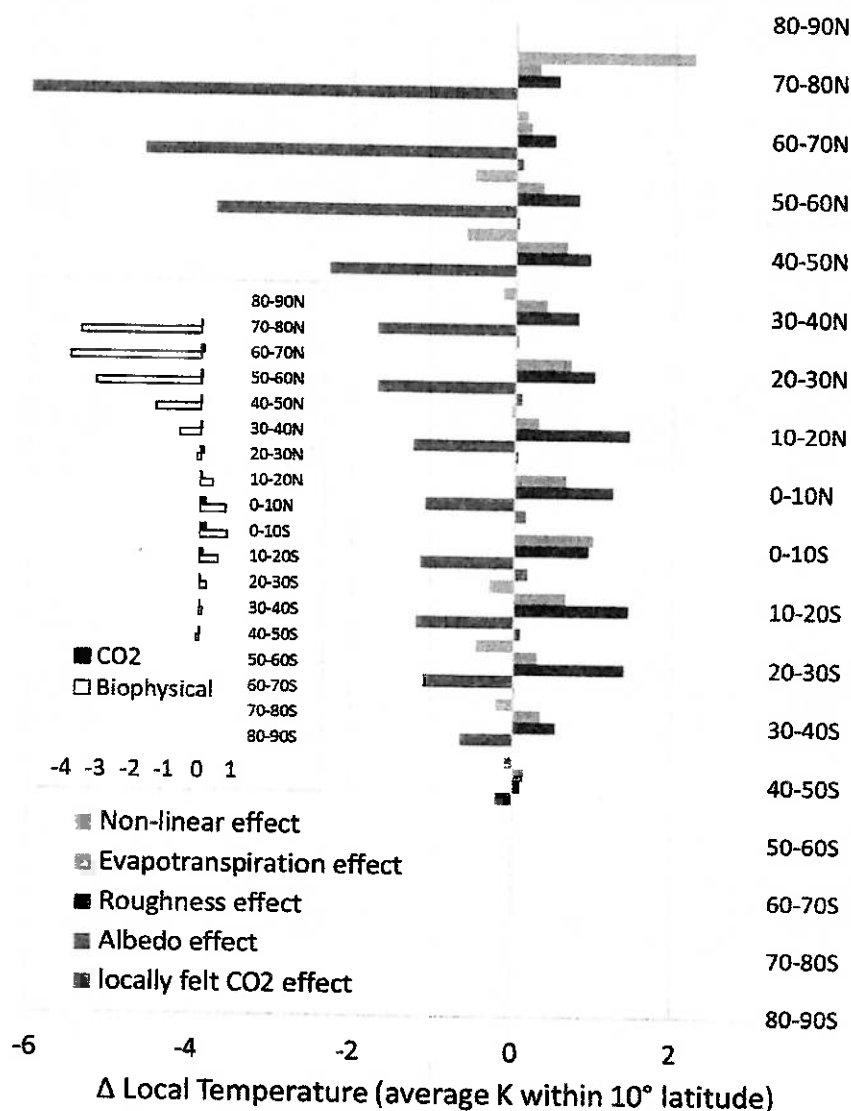


FIGURE 4 | Effect of complete deforestation on local annual temperature by climate factor, averaged across the land surface within a 10° latitudinal band. Complete deforestation was implemented globally and analyzed by 10° latitudinal bands (Davin and de Noblet-Ducoudré, 2010). The CO₂ effect was determined from total aboveground biomass in each 10° band after Walker et al. (2020) and scaled by CERA-derived sensitivity by latitude. Inset distinguishes the sum of all local biophysical effects from local CO₂ effects.

increasing temperatures, enhancing direct or indirect (cloud formation) albedo effects. This negative feedback on temperature has been observed to counter anomalous heat events in the mid-latitudes (Paasonen et al., 2013).

Some Forests Provide Global Climate Benefits Through Biophysical Effects

Disregarding the biophysical effects of specific forests on global climate means under-selling some forest actions and over-selling others. The response to local forest change is not equivalent for similar sized areas in different latitudes. According to Arora and Montenegro (2011) warming reductions per unit reforested area

are three times greater in the tropics than in the boreal and northern temperate zone due to a faster carbon sequestration rate magnified by year-round biophysical cooling. Thus, considering biophysical effects significantly enhances both the local and global climate benefits of land-based mitigation projects in the tropics (see Figures 4, 5).

Constraints on Forest Climate Benefits in the Future

Climate change is likely to alter the biophysical effect of forests in a variety of ways. Deforestation in a future (warmer) climate could warm the tropical surface 25% more than deforestation

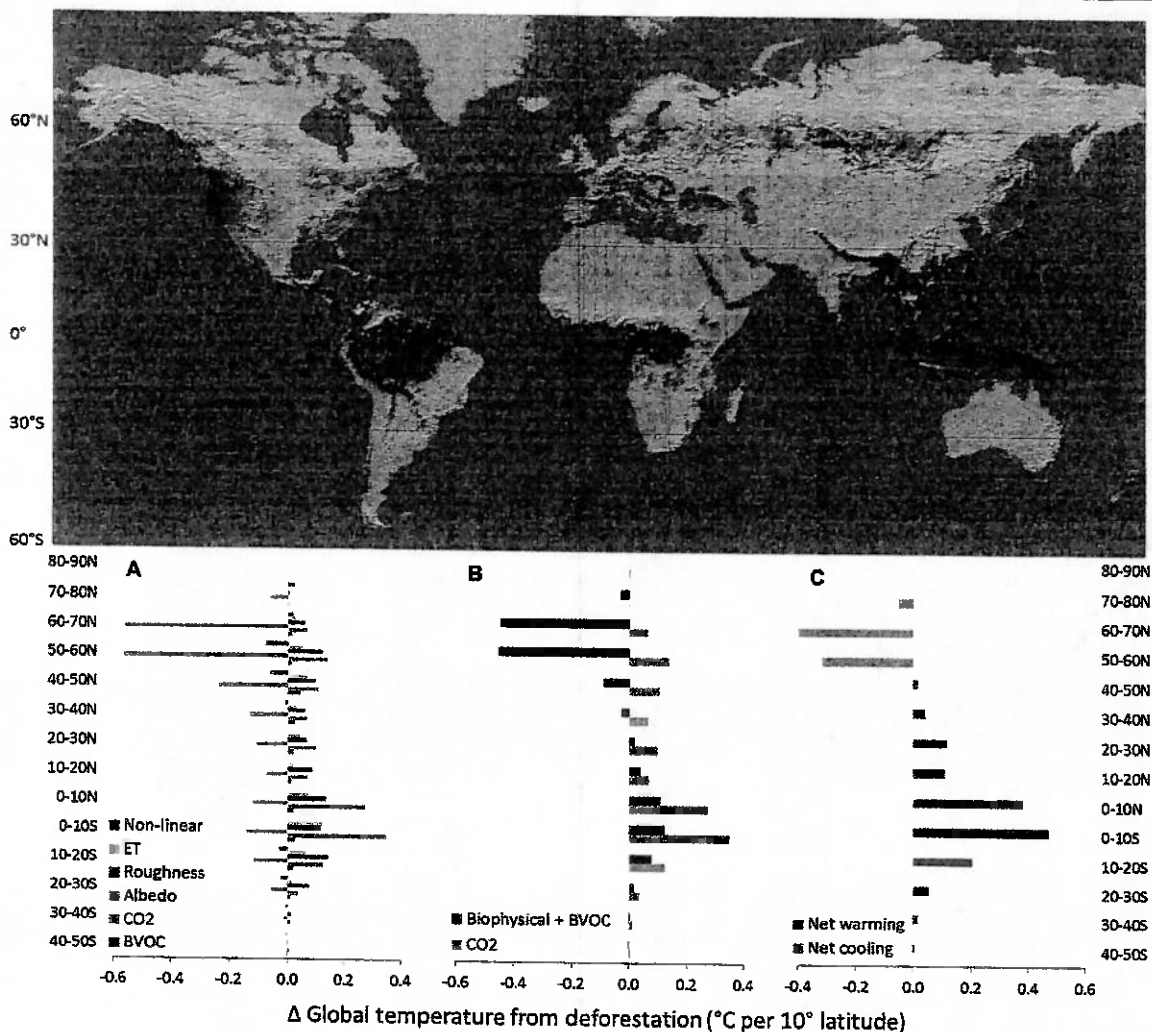


FIGURE 5 | Effect of complete deforestation on global temperature by 10° band of latitude. **(A)** Contribution to global temperature change by climate forcing factor. Biophysical factors are from Davin and de Noblet-Ducoudré, 2010, area-weighted. BVOC effects are estimated relative to albedo effects based on Scott et al., 2018. CO₂ effect is based on aboveground live biomass for each 10° latitudinal band following Baccini et al., 2017 and Walker et al., 2020. **(B)** Net biophysical and BVOC effect versus CO₂ effect. **(C)** Cooling or warming effects of deforestation by 10° latitudinal band (BVOC included). "Forests as mountains" map of aboveground biomass carbon in woody vegetation ca. 2016 courtesy of Woodwell Climate Research Center and shaded to indicate where deforestation results in net global warming. See **Supplementary Information 1** for details.

in a present-day climate due to stronger decreases in turbulent heat fluxes (Winckler et al., 2017b). In a warmer climate, reduced snow cover in the temperate and boreal regions will lead to a smaller albedo effect and thus less biophysical cooling with high latitude deforestation. In addition to snow cover change, future rainfall regimes will affect the response of climate to changes in forest cover (Pitman et al., 2011) as rainfall limits the supply of moisture available for evaporative cooling. Increases in water use efficiency due to increasing atmospheric CO₂ may reduce evapotranspiration (Keenan et al., 2013), potentially reducing the local cooling effect of forests and altering atmospheric moisture content and dynamics at local to global scales. Future BVOC production may increase due to warming and simultaneously decline due to CO₂ suppression

(Lathière et al., 2010; Unger, 2014; Hantson et al., 2017). The physiological and ecological responses of forests to warming, rising atmospheric CO₂ and changing precipitation contribute to uncertainty in the biophysical effect of future forests on climate.

Forest persistence is essential for maintaining the global benefits of carbon removals from the atmosphere and the local and global benefits of the physical processes described above. Changing disturbance regimes may limit forest growth and regrowth in many parts of the world. Dynamic global vegetation models currently show an increasing terrestrial carbon sink in the future. This sink is thought to be due to the effects of fertilization by rising atmospheric CO₂ and N deposition on plant growth as well as the effects of climate change lengthening the growing season in northern temperate and boreal areas (Le Quéré et al.,

2018). Free-air carbon dioxide enrichment (FACE) experiments often show increases in biomass accumulation under high CO₂ but results are highly variable due to nutrient limitations and climatic factors (Feng et al., 2015; Paschalis et al., 2017; Terrer et al., 2018). Climate change effects on the frequency and intensity of pest outbreaks are poorly studied, but are likely to be significant, particularly at the margins of host ranges. Warmer springs and winters are already increasing insect-related tree mortality in boreal forests through increased stress on the tree hosts and direct effects on insect populations (Volney and Fleming, 2000; Price et al., 2013).

Climate also affects fire regimes. In the tropics, fire regimes often follow El Niño cycles (van der Werf et al., 2017). As temperatures increase, however, fire and rainfall are decoupled as the flammability of forests increases even in normal rainfall years (Fernandes et al., 2017; Brando et al., 2019). Fire frequency is also increasing in some temperate and boreal forests, with a discernable climate change signal (Abatzoglou and Williams, 2016). Modeling exercises indicate that this trend is expected to continue with increasing damage to forests as temperatures rise and fire intensity increases (De Groot et al., 2013).

In addition to changes induced by warming, continued deforestation could severely stress remaining forests by warming and drying local and regional climates (Lawrence and Vandecar, 2015; Costa et al., 2019; Gatti et al., 2021). In the tropics, a tipping point may occur, potentially resulting in a shift to shorter, more savannah-like vegetation and altering the impact of vast, previously forested areas on global climate (Nobre et al., 2016; Brando et al., 2019). Some of these processes are included in climate models and some are not. The gaps leave considerable uncertainty. Nevertheless, a combination of observations, models, and theory gives us a solid understanding of the biophysical effects of forests on climate at local, regional and global scales. We can use that knowledge to plan forest-based climate mitigation and adaptation.

Mitigation Potential of Forests: Beyond the Carbon/Biophysical Divide

If instead of focusing on the contrast between biophysical and biochemical impacts of forests and forest loss, we focus on the potential of forests to cool the planet through both pathways, another picture emerges. By our conservative estimate, through the combined effects on CO₂, BVOC, roughness and evapotranspiration, forests up to 50°N provide a net global cooling that is enough to offset warming associated with their low albedo. Given the most realistic pathways of forest change in the future (not complete deforestation of a 10° latitudinal band, or an entire biome), global climate stabilization benefits likely extend beyond 50°N. For the 29% of the global land surface that lies beyond 50°N, forests may warm the planet, but only as inferred from assessing the effects of complete zonal deforestation with all the associated, and powerful, land-ocean feedbacks spawned by largescale forest change in the boreal zone. Forests above 50°N, like forests everywhere, provide essential local climate stabilization benefits by reducing surface temperatures during

the warm season as well as periods of extreme heat or drought. Indeed, they also reduce extreme cold.

Creating a fair and effective global arena for market-based solutions to climate change requires attention to all the ways that forests affect climate, including the biophysical effects. Future metrics of forest climate impacts should consider the effects of deforestation beyond CO₂. Only recently have modelers begun to include BVOC. Doing so means that the albedo of intact forests (or the atmosphere above them) is higher due to the creation of SOA and subsequent cloud formation. Modeled deforestation thus results in less of a change in albedo, reducing the biophysical cooling effect. Similarly, accounting for the ozone and methane effects of BVOC reduces the biogeochemical warming from deforestation (Scott et al., 2018). In addition, especially in the tropics, deforestation reduces the strength of the soil CH₄ sink (Dutaur and Verchot, 2007). While a small change relative to the atmospheric pool of CH₄ (the second most important greenhouse gas), the loss of this sink is equivalent to approximately 13% of the current rate of increase in atmospheric CH₄ (Saunois et al., 2016). We already have the data (Figure 5) to begin conceptualizing measures to coarsely scale CO₂ impacts of forest change by latitude. Finer resolution of latitude, background climate (current and future) and forest type would improve any such new, qualifying metric for the climate mitigation value of forests.

The role of forests in addressing climate change extends beyond the traditional concept of CO₂ mitigation which neglects the local climate regulation services they provide. The biophysical effects of forest cover can contribute significantly to solving local adaptation challenges, such as extreme heat and flooding, at any latitude. The carbon benefits of forests at any latitude contribute meaningfully to global climate mitigation. In the tropics, however, where forest carbon stocks and sequestration rates are highest, the biophysical effects of forests amplify the carbon benefits, thus underscoring the critical importance of protecting, expanding, and improving the management of tropical forests. Perhaps it is time to think more broadly about what constitutes global climate mitigation. If climate mitigation means limiting global warming, then clearly the biophysical effects of deforestation must be considered in addition to its effects on atmospheric CO₂. We may further consider whether mitigation is too narrow a scope for considering the climate benefits provided by forests. Climate policy often separates mitigation from adaptation, but the benefits of forests clearly extend into both realms.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

DL conceived the presented idea. All authors helped perform the computations, discussed the results, and contributed to the final manuscript.

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Patterns of Consumption and Diet Differentiation for Three Breeding Warbler Species During a Spruce Budworm Outbreak

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ABSTRACT.—Diets of three warbler species were analyzed during a spruce budworm outbreak in the boreal forest of northern Ontario. Beetles constituted a large portion of the food items consumed by Cape May (*Dendroica tigrina*), Bay-breasted (*Dendroica castanea*), and Tennessee (*Vermivora peregrina*) warblers early in the breeding season (7-11 June), and caterpillars were the most frequently used food category shortly later (18-24 June). Differences in diet served to differentiate the warbler species in the earlier period when Bay-breasted Warblers consumed more beetles, Tennessee Warblers consumed more caterpillars, and Cape May Warblers consumed more flies than the other species. Only Bay-breasted Warblers' continuing preference for beetles differentiated the warblers' diets in the later period. Food-niche overlaps increased for two of the three warbler species pairs between the two periods in June, but there was no change in the overlap between Bay-breasted and Cape May warbler diets.

RESUMEN.—Se analizaron las dietas de tres especies de parúlidos insectívoros durante la erupción del gusano del abeto en los bosques boreales del nor-

te de Ontario, Canadá. Durante el primer período de la época reproductiva (7-11 junio), una gran proporción de los ítems alimenticios consumidos por *Dendroica tigrina*, *D. castanea* y *Vermivora peregrina* consistió en escarabajos, mientras que más tarde (18-24 junio) el ítem alimenticio consumido con mayor frecuencia fue orugas. Las diferencias en la dieta sirvieron para diferenciar las tres especies de parúlidos durante el período inicial, cuando *D. castanea* consumió más escarabajos, *V. peregrina* consumió más orugas y *D. tigrina* consumió más moscas con relación a las otras especies. Durante el período más tardío, la dieta sólo se diferenció entre las tres especies por la continuación de la preferencia de escarabajos por parte de *D. castanea*. La superposición de los nichos alimenticios aumentó para dos de los tres pares de especies entre los dos períodos en junio, pero no hubo cambios en la superposición de la dieta entre *D. castanea* y *D. tigrina*.

There have been few systematic studies of warblers' diets during their breeding season. Historical reports were anecdotal, based on collection of a limited number of individual birds and generating a simple list of food items found in gizzards (e.g. Bent 1963). Busby and Sealey (1979), Holmes and Robinson (1988), and Cooper et al. (1990) performed quan-

titative studies of the breeding season knowledge of forest warblers through their own field research. Quantitative studies of two warbler species by Crawford (1952) which provided food items other than Quantitative accounts (*Vermivora peregrina* 1998) are largely (1996). Little further the diets of these t

Efforts to define species have traditional behavior and habitat cause of difficulty. Coarse-scale habitat or tree species static during a breeding season of food resources for that there is little food niche overlap diets of warbler species breeding season or time. Existence of forest warblers would sight into coexistence. We therefore examined Cape May, and measured food-niche species, and determined breeding season. We diets of the three warblers by the type of prey breeding season.

Study Area and Methods. Cape May, and Bay-breasted during a spruce budworm outbreak in Ontario (49°47' N, 80°47' W). Three warbler species were selected for study site, and because of large spruce budworm outbreaks in the area, Jennings and Crawford (1996) found that area is predominantly white spruce (*Populus* spp.) and tamarack (*Larix laricina*) at least 50% balsam poplar host trees of spruce forest. This is a larger project that could be studying heights or loca-

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titative studies of Neotropical migrants' diets during the breeding season, but none included the boreal forest warblers that were the focus of this study. Current knowledge of the diets of Cape May (*Dendroica tigrina*; Baltz and Latta 1998) and Bay-breasted (*D. castanea*; Williams 1996) warblers during the breeding season comes from descriptive reports identifying primarily lepidopteran larvae and other invertebrates. Quantitative analysis of the diets of these two warbler species relies almost exclusively on research by Crawford and Jennings (1989) and Mitchell (1952) which provide little data on consumption of food items other than spruce budworm larvae. Quantitative accounts of the Tennessee Warbler's (*Vermivora peregrina*) diet (Rimmer and McFarland 1998) are largely based on data from McMartin (1996). Little further information exists regarding the diets of these three warbler species.

Efforts to define the ecological niches of warbler species have traditionally focused on foraging behavior and habitat use (MacArthur 1958), in part because of difficulties associated with diet studies. Coarse-scale habitat measures, such as forest structure or tree species composition, can be considered static during a breeding season, whereas abundance of food resources for birds may change over time so that there is little reason to assume that extent of food niche overlap is static. Thus, we do not know if diets of warbler species are differentiated during the breeding season or if diets change within that brief time. Existence of diet differentiation among boreal forest warblers would provide an important new insight into coexistence of ecologically similar species. We therefore examined the composition of Tennessee, Cape May, and Bay-breasted warblers' diets, measured food-niche overlap among the warbler species, and determined if diets changed within the breeding season. We tested the hypothesis that the diets of the three warbler species are differentiated by the type of prey items they consume during the breeding season.

Study Area and Methods.—The diets of Tennessee, Cape May, and Bay-breasted warblers were examined during a spruce budworm outbreak near Longlac, Ontario (49°47'N, 86°32'W). Those warbler species were selected because they were common at the study site, and because they are important predators of large spruce budworm larvae (Morris et al. 1958, Jennings and Crawford 1985). The boreal forest in that area is predominantly balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) with extensive aspen stands (*Populus* spp.), and smaller numbers of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*). This study was conducted on three 300 ha forest blocks that consisted of at least 50% balsam fir and white spruce—primary host trees of spruce budworm. It was also part of a larger project that concluded no changes in diets, foraging heights or locations, or foraging maneuvers by

Tennessee and Bay-breasted warblers were attributable to insecticide applications (McMartin 1996). Data from both treated and control blocks were combined and are used here.

Territorial males were collected under a Canadian Wildlife Service permit with the help of recorded songs of conspecific males. Selecting only males eliminated possible biases from diet differences based on sex. The first sample from 7–11 June 1994 corresponded to the early breeding season when pair formation and nest building were occurring. The second sample from 18–24 June 1994 corresponded to the mid-breeding season when egg-laying and incubation were underway. The study concluded before most adults began feeding young because insecticide-induced reductions in caterpillar populations were expected to have the greatest effect on warblers during the second sampling period. One milliliter of 70% ethanol was injected into the digestive tract of each bird through the esophagus to prevent continued digestion of the gizzard contents. The carcasses were stored in portable coolers in the field, and gizzards were removed and stored in alcohol later the same day. After completion of field work, gizzard contents were flushed out, and individual food items were counted and identified to order. Even though gizzard contents were generally fragmented, it was possible to estimate minimum number of each type of food item present by counting heads, head capsules and whole bodies, and by matching pairs of wings, elytra, and mandibles. Food items were assumed to represent prey taken sometime during the last 2 h a bird lived because gizzards of small insectivorous birds are almost empty 2 h after feeding if no further food is taken (Mook and Marshall 1965, Custer and Piteika 1974). Counts of food category items were highly skewed, and could not be normalized, so a Kruskal-Wallis test was used to determine if the diet of each warbler species changed between the early and midbreeding season periods.

Food-niche breadth was calculated for each warbler species during the early and midbreeding season periods using Levin's standardized measure, B_i . Morisita's index of similarity (C) was used to provide an unbiased measure of food-niche overlaps between pairs of species (Krebs 1989). Jack-knife estimates of standard deviation were used to determine if changes in niche overlap between the two collection periods were significant. We used logistic regression to determine if diets of the three warbler species could be differentiated by their consumption of items from different food categories during the 7–11 June and 18–24 June periods. SAS proc CATMOD (SAS Institute 1985) provided a distribution-free statistical test of diet differentiation for highly skewed data that made distribution-sensitive tests inappropriate.

Results.—Over 2,000 food items were classified to order from 283 warbler gizzards that were collected

TABLE 1. Diet differentiation among Bay-breasted, Cape May, and Tennessee warblers during early (7–11 June) and mid-breeding season (18–24 June) in northern Ontario, based on maximum-likelihood analysis of variance. Mean number of food items per gizzard are shown, with percentages in parentheses constituting each food category for each species.

	χ^2	P	Mean number of food items per gizzard (% of total)		
			Bay-breasted	Cape May	Tennessee
Early breeding season					
Number of gizzards			49	25	45
Coleopteran adults	12.22	0.0022	5.3 (75.7%)	3.9 (52.7%)	2.7 (41.5%)
Lepidopteran larvae	12.96	0.0015	0.4 (5.7%)	1.3 (17.6%)	3.1 (47.7%)
Diptera	8.76	0.0125	0.6 (8.6%)	1.4 (18.9%)	0.3 (4.6%)
Araneae	0.97	NS	0.2 (2.9%)	0.2 (2.7%)	0.1 (1.5%)
Other ^a	1.52	NS	0.5 (7.1%)	0.6 (8.1%)	0.3 (4.6%)
Mid-breeding season					
Number of gizzards			59	45	60
Coleopteran adults	15.11	0.0005	2.1 (29.6%)	0.8 (8.8%)	0.5 (5.8%)
Lepidopteran larvae	5.47	NS	4.1 (57.7%)	7.2 (79.1%)	6.9 (80.2%)
Diptera	3.30	NS	0.4 (5.6%)	0.4 (4.4%)	0.2 (2.3%)
Araneae	3.67	NS	0.2 (2.8%)	0.5 (5.5%)	0.3 (3.5%)
Other	2.51	NS	0.3 (4.2%)	0.2 (2.2%)	0.7 (8.1%)

^a Other food includes Homoptera, Hymenopteran adults and larvae, Hemiptera, Coleopteran larvae, Gastropoda, Odonata, Trichoptera, and Neuroptera

(Table 1). A larger number of prey items may have been present, but the state of fragmentation of arthropods found in the warblers' gizzards made counting and identification of additional prey items unreliable. Of those food items, 85.7% were either coleopteran adults or lepidopteran larvae, and Diptera and Araneae accounted for a further 8.8% of the total. Nine other food categories represented in very low numbers were pooled as "other food" for statistical analysis.

Of the five major food categories, Bay-breasted Warblers consumed predominantly coleopteran adults (75.7%) early in the breeding season, with no other food category constituting more than 10% of the total (Table 1). Just two weeks later, the diet consisted of 29.6% coleopteran adults and 57.7% lepidopteran larvae. The increase in consumption of lepidopteran larvae ($F = 80.97$, $P = 0.0001$) and decrease in consumption of coleopteran adults ($F = 49.86$, $P = 0.0001$) between 7–11 June and 18–24 June were statistically significant, whereas consumption of Diptera also declined significantly ($F = 4.21$, $P = 0.0426$).

Cape May Warblers' diet was less dominated by coleopteran adults early in the breeding season (52.7%) than the diet of Bay-breasted Warblers, but Cape May Warblers shifted to a diet of 79.1% lepidopteran larvae during the midbreeding season (Table 1). There were significant decreases in consumption of coleopteran adults ($F = 57.90$, $P = 0.0001$) and increases for lepidopteran larvae ($F = 92.45$, $P = 0.0001$), whereas consumption of Diptera ($F = 5.99$, $P = 0.0170$) and other food also declined ($F = 7.42$, $P = 0.0082$) between the early and midbreeding season.

Early in the breeding season, coleopteran adults represented 41.5% of the Tennessee Warblers' diet, whereas lepidopteran larvae were 47.7% (Table 1). As with the other two species, use of coleopteran adults dropped significantly ($F = 58.65$, $P = 0.0001$), whereas consumption of lepidopteran larvae increased to 80.2% of the diet in the later period ($F = 58.11$, $P = 0.0001$).

Standardized food-niche breadth for Bay-breasted Warblers doubled from early to midbreeding season, but declined by two-thirds for Cape May and Tennessee warblers over the same period (Table 2a). Cape May and Bay-breasted warblers' diets overlapped more than other warbler pairs in the early breeding season, whereas Cape May and Tennessee warbler diets overlapped most in the midbreeding season (Table 2b). Food-niche overlap between Bay-breasted and Cape May warblers remained static from early to midbreeding season, but overlaps between other pairs of warbler species increased over the two periods. Morisita's C rose from 0.43 in the early period to 0.60 in the later period for Bay-breasted and Tennessee warblers, and from 0.44 to 0.78 for Cape May and Tennessee warblers.

The warbler species differed in their consumption of coleopteran adults ($\chi^2 = 12.22$, $P = 0.0022$), lepidopteran larvae ($\chi^2 = 12.96$, $P = 0.0015$) and Diptera ($\chi^2 = 8.76$, $P = 0.0125$), in the early breeding season (Table 1). Bay-breasted Warblers consumed more beetles, Cape May Warblers consumed more flies, and Tennessee Warblers consumed more caterpillars than other warbler species between 7–11 June. Later in the breeding season, from 18–24 June, only cole-

TABLE 2. Food-niche overlap

Bay-breasted Warbler
Cape May Warbler
Tennessee Warbler

Bay-breasted: Cape May
Bay-breasted: Tennessee
Cape May: Tennessee

olepteran adults (χ^2) differentiate the warblers again consume warbler species (1)

Discussion.—Diet was extensive as there were differences and flies by the composition reflecting strategies. For example, Tennessee caterpillars in that extensive probing leaf-rolling caterpillar consistent with Grabe extensive probing for during spring migration of beetles and Cape 7–11 June could represent different locations (1958), but additional confirm differences microsites. Relative larvae early in June breasted warblers spruce budworm spruce budworm period are rarely consumed they are hidden when detected (Jennings) and therefore may be a resource.

Later in the breeding season, the diet of Bay-breasted Warblers differed among beetles. That may be of lepidopteran larvae that period, and spruce budworm larvae reduced the number on one treated by populations of spruce budworm background levels and Jennings 1989

TABLE 2. Food-niche metrics including (a) Levin's standardized niche breadth (B_n), and (b) Morisita's measure of overlap ($C \pm SD$) between pairs of warbler species during the early and mid-breeding season.

	Early breeding season (7–11 June)	Mid-breeding season (18–24 June)
(a) Standardized food niche breadth, Levin's B_n		
Bay-breasted Warbler	0.162	0.329
Cape May Warbler	0.447	0.135
Tennessee Warbler	0.369	0.125
(b) Paired comparisons, Morisita's C		
Bay-breasted: Cape May	0.604 $\pm$ 0.006	0.604 $\pm$ 0.006
Bay-breasted: Tennessee	0.434 $\pm$ 0.006	0.603 $\pm$ 0.006
Cape May: Tennessee	0.441 $\pm$ 0.010	0.777 $\pm$ 0.008

opteran adults ($\chi^2 = 15.11$, $P = 0.0005$) served to differentiate the warblers' diets with Bay-breasted Warblers again consuming beetles more than the other warbler species (Table 1).

Discussion.—Diet differentiation among warblers was extensive early in the breeding season, when there were differences in use of beetles, caterpillars, and flies by the three species. Differences in diet composition reflect to some extent differences in foraging strategies and locations used by the warblers. For example, Tennessee Warblers' consumption of caterpillars in that period can be explained in part by extensive probing of alder (*Alnus* spp.) foliage for leaf-rolling caterpillars (McMartin 1996). That is consistent with Graber and Graber's (1983) record of extensive probing for leafrollers by Tennessee Warblers during spring migration. Bay-breasted Warblers' use of beetles and Cape May Warblers' use of flies from 7–11 June could reflect their tendencies to forage in different locations within the canopy (MacArthur 1958), but additional research would be needed to confirm differences in prey-type abundance among microsites. Relatively limited use of lepidopteran larvae early in June, especially by Cape May and Bay-breasted warblers, may be explained in part by spruce budworm phenology. The smaller instars of spruce budworm that were present during this period are rarely consumed by birds, either because they are hidden within buds, avoided or simply not detected (Jennings and Crawford 1985, Morse 1989) and therefore may not qualify as a potential food resource.

Later in the breeding season, only the use of beetles differed among the three species, with Bay-breasted Warblers maintaining their preference for beetles. That may be attributed to the dominant use of lepidopteran larvae by all three species during that period, and to the superabundance of spruce budworm larvae even after insecticide application reduced the number of lepidopteran larvae by 86% on one treated block (McMartin 1996). Outbreak populations of spruce budworm can be over 70 $\times$ background levels in nonepidemic years (Crawford and Jennings 1989), and the spruce budworm pop-

ulation at Longlac was expected to be at an epidemic level. As a result, large, accessible spruce budworm larvae were probably still abundant in late June, and were not a limiting resource even though the total number of caterpillars had dropped. All three warbler species included caterpillars in their fundamental niches, but did not compete for a resource that was effectively unlimited, so that there was no need to segregate diet among those species while the budworm larvae were still available. The different extent of diet differentiation between the two periods suggests that selection of food categories is less likely to be meaningful as a dimension of niche definition when a major food resource is superabundant.

The changes in food consumption between 7–11 June and 18–24 June were remarkable, with increasing consumption of lepidopteran larvae for all three warbler species. Coleopteran adults formed a large part of the diets of all three warbler species early in the breeding season, but their importance as a food resource was much reduced just two weeks later. Diet overlaps in late June were over the 0.6 level considered to be biologically significant (Zaret and Rand 1971); however, it is not surprising to find high food-niche overlaps at the same trophic level during a brief period when one high-energy food resource, spruce budworm larvae, is readily available in great numbers. These boreal forest warblers all exploited that resource while it was abundant.

An in-depth understanding of use of food resources by coexisting warbler species is only starting to be revealed, and our results show that analysis of warbler diets during the breeding season requires a dynamic approach. Relative use of different food resources changes over a short time, and as a result food-niche overlaps among warblers change, at least in boreal forest habitat where an insect pest has reached unusually high densities. Diet serves as a niche dimension at some times, but can be less meaningful when one food resource is superabundant. Those changes highlight the complexity of diet analysis for the three warbler species.

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during early (7–11 June) and mid-breeding (18–24 June) seasons. Percentages in parentheses are standardized to the total diet.

Standardized (% of total)

Tennessee

45
2.7 (41.5%)
3.1 (47.7%)
0.3 (4.6%)
0.1 (1.5%)
0.3 (4.6%)

60
0.5 (5.8%)
6.9 (80.2%)
0.2 (2.3%)
0.3 (3.5%)
0.7 (8.1%)

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Pauli (Canadian Wildlife Service), Hans Lefebvre, Jennifer Lukianchuk, Erin Nixon, Heather Pollard and Lynn Schriml helped in the collection and processing of birds for diet analysis. Funding was provided by the Wildlife Toxicology Fund—a joint project of the World Wildlife Fund, Environment Canada, and the Natural Sciences and Engineering Council, Canadian Forest Service, Canadian Wildlife Service, Spray Efficacy Research Group, Ontario Ministry of Natural Resources, Société de protection des forêts contre les insectes et maladies, Forest Protection Limited, Rohm and Haas Canada Inc., Novo Nordisk Bioindustrials Inc., and the University of Toronto.

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The Auk 119(1):

Growth and

SHANNON
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³Ontario

ABSTRACT.—I Geese (*Branta* Geese (*Chen ca* to evaluate if g terns differed i such difference: of the growth p torically experi of growth and Snow goose go: for other Arcti growth rates an structures, dig were observed pared to Canad locomotion and generally increa more developa Geese. Relative and body mass a physiological terns of growtl plained as adap growing season conditions, histor species.

RESUMEN.—C adultos de *Br* diense) y *Chen* Nieve Menor) p y los patrones c y para determin plicadas por la o por las condic tóricamente por crecimiento y d *rulescens* fueron para otros gans ferencias entre vas de crecimie tructuras exteri esqueléticos. C del cuerpo asoc ción y procesar

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**Partners In Flight
Bird Conservation Plan
Montana**

VERSION 1.1

Montana Partners In Flight
April 2000

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Montana Priority Levels

We assigned each of the 141 species in Table 2 to one of the following four priority levels. All species designated as levels I-III are treated in this plan. Generally, level I species are the highest priority and are the focus of proposed conservation actions. Most biological objectives are integrated, however, and address multiple species needs. The names of these levels (e.g. "Conservation Action") should not therefore be considered mutually exclusive.

- I. **Conservation Action.** Generally high overall scores (>22), declining population trends (PT/PTU of 5/1 or 5/2), and/or high area importance (PA % Pop. >20). These are the species for which Montana has a clear obligation to implement conservation
- II. **Monitoring Species.** Species in need for which we have responsibility, but with lesser threat or stable/increasing populations in the state. As compared to level I, these species have generally lower overall scores, in many cases because they are poorly sampled by the BBS. Montana has a high responsibility to monitor the status of these species, and/or to design conservation actions.
- III. **Local Concern.** Species of concern (often designated as such by participating agencies) which rank lower, are not in imminent risk, or which are near-obligates for high priority habitat. Presence of these species may serve as added criteria in the design and selection of conservation or monitoring strategies.
- IV. **Non-Priority.** Formerly suggested for inclusion in the planning effort, but recommended for deletion because of occurrence as rare migrants only, extremely peripheral occurrence, or lack of imminent risk (widespread, generalist, increasing).

BIRD CONSERVATION PRIORITIES IN MONTANA

Priority Bird Species List

Our prioritization process led to the selection of the following 107 species (one group) that merited priority status in the state. These included 14 species at priority level I, 43 at level II, and 51 level III, or "local concern" species:

Level I (n=14)

Common Loon
Trumpeter Swan
Harlequin Duck
Sage Grouse
Piping Plover
Mountain Plover
Interior Least Tern
Flammulated Owl
Burrowing Owl
Black-backed Woodpecker
Olive-sided Flycatcher
Brown Creeper
Sprague's Pipit
Baird's Sparrow

Level II (n=43)

Horned Grebe
White-faced Ibis
Barrow's Goldeneye
Hooded Merganser
Bald Eagle
Northern Goshawk
Ferruginous Hawk
Peregrine Falcon
Ruffed Grouse
Columbian Sharp-tailed Grouse
Long-billed Curlew
Marbled Godwit
transient shorebirds
Franklin's Gull
Caspian Tern
Common Tern
Forster's Tern
Black Tern
Black-billed Cuckoo
Yellow-billed Cuckoo
Black Swift

Vaux's Swift
Calliope Hummingbird
Lewis's Woodpecker
Red-headed Woodpecker
Red-naped Sapsucker
Williamson's Sapsucker
Three-toed Woodpecker
Pileated Woodpecker
Willow Flycatcher
Hammond's Flycatcher
Cordilleran Flycatcher
Winter Wren
Veery
Loggerhead Shrike
Red-eyed Vireo
Lazuli Bunting
Brewer's Sparrow
Lark Bunting
Grasshopper Sparrow
McCown's Longspur
Chestnut-collared Longspur
Black Rosy-finch

Level III (n=51)

Clark's Grebe
American White Pelican
American Bittern
Black-crowned Night-heron
Northern Harrier
Sharp-shinned Hawk
Swainson's Hawk
Blue Grouse
White-tailed Ptarmigan
Yellow Rail
Killdeer
Black-necked Stilt
Willet
Wilson's Phalarope
Eastern Screech-owl
Western Screech-owl

Great Gray Owl
Boreal Owl
Short-eared Owl
Common Poorwill
Chimney Swift
Rufous Hummingbird
Downy Woodpecker
Least Flycatcher
Clark's Nutcracker
Chestnut-backed Chickadee
Sedge Wren
American Dipper
Golden-crowned Kinglet
Townsend's Solitaire
Varied Thrush
Gray Catbird
Sage Thrasher
Cassin's Vireo
Plumbeous Vireo
Warbling Vireo
Nashville Warbler
Townsend's Warbler
Ovenbird
American Redstart
MacGillivray's Warbler
Green-tailed Towhee
Chipping Sparrow
Clay-colored Sparrow
Lark Sparrow
LeConte's Sparrow
Nelson's Sharp-tailed Sparrow
Song Sparrow
Bobolink
Red-winged Blackbird
Yellow-headed Blackbird
Brewer's Blackbird
Orchard Oriole
Cassin's Finch
Red Crossbill

Table 2. Bird species considered for priority status by Montana PIF, with assigned priority levels, CBO priority scores, population trend, percent population within physiographic areas, and special status.

Species	Priority	CBO Score		BBS Population Trend (PT/PTU)		Percent Population		Special Status	Comments
		PA 64	PA39	PA 64	PA39	PA 64	PA39		
Common Loon	I	16	-	2/4				SNBF	MT Score = 19
Clark's Grebe	III	19	20	3/8	3/8			N	Colonial
Horned Grebe	II		20	3/7	5/2		37.3		
American White Pelican	III	22	21	3/6	3/6	16.3		N	Colonial
American Bittern	III	17	18	3/6	4/3				
Black-crowned Night-heron	III	13	14	3/8	3/6			N	Colonial
White-faced Ibis	II	15	16	3/8	3/8			SNB	Colonial
Trumpeter Swan	I	26	26	3/7	3/8	10		SNBFW	T&E
Harlequin Duck	I	-	-	3/8				SNBF	MT Score=21
Barrow's Goldeneye	II	24		3/5		35.5			
Hooded Merganser	II	22		3/7	3/8	24.1			
Osprey	IV	16		2/4	3/8	24.9			
Bald Eagle	II	16	19	2/4	3/8			SNF	T&E
Northern Harrier	III		17	2/1	2/1		25.6		
Sharp-shinned Hawk	III	18		3/6	3/8	32.4			
Northern Goshawk	II	21	19	4/3	3/8			SNB	Managemnt concern
Swainson's Hawk	III		20	2/2	2/4		20.9	B	
Ferruginous Hawk	II	22	20	3/6	1/1	10.5	26.7	SNBF	Special concern
Peregrine Falcon	II	18	19	3/7	3/8			SNF	T&E
Blue Grouse	III	24		5/2	3/8	14.2			
White-tailed Ptarmigan	III	22		3/8					
Ruffed Grouse	II	21		5/1	3/7	10.0			
Sage Grouse	I	23	25	3/8	3/5	25.0	33.0		
(Col.) Sharp-tailed Grouse	II	-	-	3/7				SNBF	Special concern
Yellow Rail	III	-	24		3/8			NW	Peripheral sp.?
Whooping Crane	IV	-	-					SNF	T&E migrant
Piping Plover	I	-	26		3/8			SN	T&E
Killdeer	III	18	18	5/1	5/1				
Mountain Plover	I	25	27	3/8	3/8			SNBFW	Special concern
Black-necked Stilt	III	-	15		3/8			N	Colonial
Willet	III		18	3/6	2/1		22.6	W	
Upland Sandpiper	IV	19	20	3/7	3/5				
Long-billed Curlew	II	20	23	1/2	4/4	10.5	18.9	SBW	
Marbled Godwit	II		23	3/8	2/1		49.1		
Wilson's Phalarope	III	19	19	2/2	2/1	5.4	28.5		MT Score=21
Transient Shorebirds	II	-	-						multiple species
Franklin's Gull	II	22	24	3/7	5/2	8.2	8.0	SNW	Colonial
Caspian Tern	II	15	14	3/8	3/8			SN	Colonial
Common Tern	II	14	14	3/8	3/6			SN	Colonial

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Species	Priority	CBO Score		BBS Population Trend (PT/PTU)		Percent Population		Special Status	Comments
		PA 64	PA39	PA 64	PA39	PA 64	PA39		
Forster's Tern	II	20	19	3/7	3/8			N	Colonial
(Interior) Least Tern	I	-	17		3/8			SN	T&E
Black Tern	II	17	19	2/3	4/4			SNB	Colonial
Black-billed Cuckoo	II	17	19	3/7	3/6				
Yellow-billed Cuckoo	II	18	19	3/8	3/7			SN	
Flammulated Owl	I	22	-	3/8				SNBF	MT Score=24
Eastern Screech-owl	III	17	17	3/8	3/8			P	
Western Screech-owl	III	19	-	3/8				P	
Northern Hawk-owl	IV	17	-	3/8					Peripheral species
Burrowing Owl	I	17	21	3/8	5/2			SNB	Special concern
Great Gray Owl	III	18	17	3/8	3/8			SNB	Managmt concern
Boreal Owl	III			3/8				SNBF	
Short-eared Owl	III	19	20	2/3	3/5		24.4	W	
Common Poorwill	III	19	19	3/8	3/7				
Black Swift	II	23	-	3/6		12.1		SNW	
Chimney Swift	III	-	16		3/8			W	
Vaux's Swift	II	22	-	3/5		41.3			
Calliope Hummingbird	II	22	20	2/1	3/8	76.0			
Rufous Hummingbird	III	19	20	1/1	3/8	18.4		W	MT Score=21
Lewis's Woodpecker	II	22	22	3/5	3/8	23.8		W	
Red-headed Woodpecker	II	18	19	3/8	3/6			W	
Red-naped Sapsucker	II	21	21	1/1	3/6	59.3	4.9		
Williamson's Sapsucker	II	22	-	3/5		47.6			
Downy Woodpecker	III		16	3/5	5/2				
Three-toed Woodpecker	II	19	18	3/6	3/8			B	
Black-backed Woodpecker	I	22	20	4/3	3/8	6.4		SNBF	Managmt concern
Pileated Woodpecker	II	14	-	2/4				B	
Olive-sided Flycatcher	I	20	17	5/1	3/7	7.0			
Western Wood-Pewee	IV	16	15	2/1	2/1	16.0			
Willow Flycatcher	II	21	19	2/1	3/6	29.8			
Least Flycatcher	III	17	15	3/5	1/1				
Hammond's Flycatcher	II	22	20	2/1	3/8	29.4			MT Score=23
Dusky Flycatcher	IV	22		2/1	3/6	32.2			MT Score=19
Cordilleran Flycatcher	II	20	21	3/5	3/6	29.1	10.5		
Cassin's Kingbird	IV	-	22		3/8			N	Peripheral species
Clark's Nutcracker	III	16	16	1/1	3/7	39.3		P	
Chestnut-backed Chickadee	III	18	-	1/2				P	MT Score=21
Brown Creeper	I	18	-	5/1	3/8	11.7		P	Managmt concern
Winter Wren	II	14	-	2/4				P	
Canyon Wren	IV	17	16	3/7	3/7			P	
Sedge Wren	III	-	21		3/8				Peripheral species

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Species	Priority	CBO Score		BBS Population Trend (PT/PTU)		Percent Population		Special Status	Comments
		PA 64	PA39	PA 64	PA39	PA 64	PA39		
American Dipper	III	21		2/2	3/8	55.4			
Golden-crowned Kinglet	III	17		2/1	3/7	22.8			
Townsend's Solitaire	III	19	18	2/1	2/4	26.5	10.9		
Varied Thrush	III	18	-	2/1				P	MT Score=20
Veery	II	17	17	2/1	3/6	8.3		W	
Gray Catbird	III	15	16	3/5	2/2			W	
Sage Thrasher	III	16	17	2/4	3/5				MT Score=19
Sprague's Pipit	I	22	24	3/7	2/1	11.6	48.1	SW	
Loggerhead Shrike	II	18	17	3/8	2/1			SBFW	Special concern
Cassin's Vireo	III	20	-	1/1					
Plumbeous Vireo	III	22	20	3/8	3/8	41.5			
Warbling Vireo	III	17	17	1/1	3/5	24.1		P	
Red-eyed Vireo	II	16	16	5/1	5/2			P	Riparian indicatr
Nashville Warbler	III	16	-	1/1		31.8			MT Score=18
Townsend's Warbler	III	19	-	1/1		44.3			MT Score=20
Ovenbird	III	19	18	3/8	2/2				
American Redstart	III	16	16	4/4				P	
MacGillivray's Warbler	III	20	19	2/4	3/6	36.0			
Lazuli Bunting	II	19	19	1/1	3/5	38.5			
Green-tailed Towhee	III	18	19	2/2	3/6	13.8		P	
Chipping Sparrow	III		16	2/1	5/1				
Clay-colored Sparrow	III	18	18	1/2	2/1	1.3	10.5	W	
Brewer's Sparrow	II	21	21	5/1	5/1	7.2	6.2	W	
Lark Sparrow	III	15	16	2/2	2/1				
Sage Sparrow	IV	22	21	3/8	3/7			BW	Peripheral sp.
Lark Bunting	II	20	18	3/6	1/1	1.0	36.7	W	
Baird's Sparrow	I	25	26	3/8	3/5	1.0	39.7	SNBFW	MT Score=27
Grasshopper Sparrow	II	20	16	5/2	1/1	1.0			
Le Conte's Sparrow	III	23	23	3/8	3/6		14.7	NBS	Special concern
N. Sharp-tailed Sparrow	III	-	26		3/8			SNW	Peripheral sp.
Song Sparrow	III	14		5/1	4/4				
McCown's Longspur	II	27	27	3/6	3/5	13.1	65.7	W	MT Score=28
Chestnut-collar Longspur	II	22	21	3/7	2/4		46.6		
Bobolink	III	19	19	3/5	2.2		1.1	W	
Red-winged Blackbird	III		14	2/1	5/1				PT/PTU = 5/1
Yellow-headed Blackbird	III	16	18	2/1	3/5				
Brewer's Blackbird	III	15		5/1	2/1	12.1			PT/PTU = 5/1
Orchard Oriole	III	-	17		3/7				

Species	Priority	CBO Score		BBS Population Trend (PT/PTU)		Percent Population		Special Status	Comments
		PA 64	PA39	PA 64	PA39	PA 64	PA39		
Black Rosy-Finch	II	22		3/8		100			
Cassin's Finch	III	19		2/4	3/7	59.8			
Red Crossbill	III	16		1/1	3/5	40.5			

Habitat Prioritization

We initiated a process for prioritizing habitats during a Montana PIF meeting in March 1997. Our philosophy was that conservation priority should be placed on those habitats that: 1) support high numbers of priority bird species; 2) are significantly threatened; 3) have shown significant historic losses; 3) support unique or particularly diverse avifauna; 4) have detailed data available; and/or 5) have good potential for implementation of conservation action.

After building species/habitat matrices (which appear in revised form in this plan at the head of each habitat section), we used a "Delphi" process to identify the highest priority subtypes in each habitat category. We used the following criteria for this effort, with average scores used as preliminary prioritization scheme: a rank of 1 was used for the habitat which most meets the intent of the criteria (e.g. has the most priority species, greatest threat, is most unique); 2 is the next highest priority, etc., with the maximum value assigned to the habitat which least meets the criteria (e.g. it comes in 5th).

Priority Species: Ranked the habitats based on the number of priority species (especially category I and II) they support.

Threat: Ranked the habitats based on threats to their quality or quantity, with a rank of 1 for the most threatened habitat.

Historic Loss: Ranked the habitats based on historic losses of acreage within the state: the habitat with the least extant habitat relative to historic levels gets a rank of 1.

Unique: Ranked the habitats based on their unique features, unique species or communities they support, relative to each.

Data Availability: Those habitats where we have the most data will likely be the ones in which we can most effectively implement conservation activities. More data = rank 1.

Conservation Potential: Ranked the habitats on the likelihood of achieving effective conservation: habitats primarily on public lands, with easily identified management issues and existing conservation impetus, would rank higher (1) than those with more nebulous potential for success.

This process led us to an additional list of high priority habitats, which was further refined as the planning process proceeded to the list of habitats treated in this plan. Within each of the five habitat categories (Grassland, Shrubland, Forest, Riparian, Wetlands) individual habitats are treated in priority order.

Development of Biological Objectives

Montana Partners 'Flight

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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 [Bulland 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.

Trees and forests

Very cool: trees stalling effects of global heating in eastern US, study finds

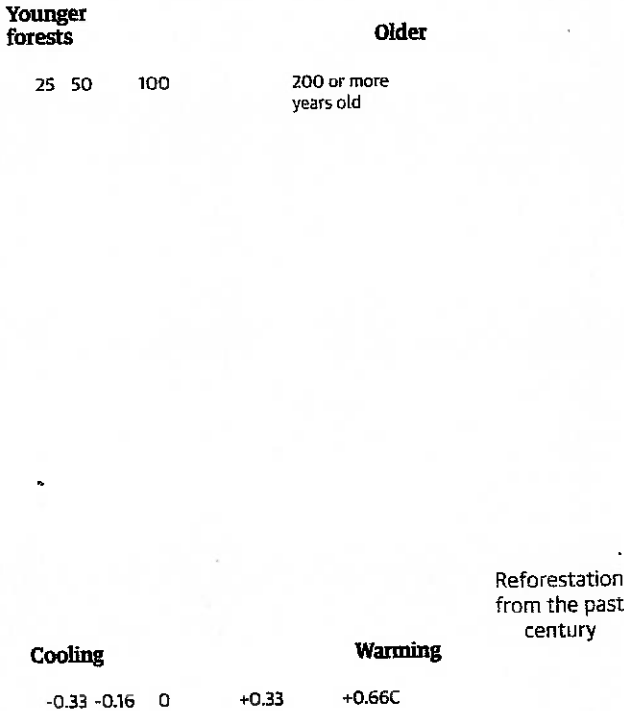
Vast reforestation a major reason for 'warming hole' across parts of US where temperatures have flatlined or cooled

Oliver Milman

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Sat 17 Feb 2024 05:00 EST

Trees provide innumerable benefits to the world, from food to shelter to oxygen, but researchers have now found their **dramatic** rebound in the eastern US has delivered a **further**, stunning feat - the curtailing of the soaring temperatures caused by the climate crisis.

While the US, like the rest of the world, has heated up since industrial times due to the burning of fossil fuels, scientists have long been puzzled by a so-called "warming hole" over parts of the US south-east where temperatures have flatlined, or even cooled, despite the unmistakable broader warming trend.



A major reason for this anomaly, the new study finds, is the vast reforestation of much of the eastern US following the initial loss of large numbers of trees in the wake of European settlement in America. Such large expanses have been reforested in the past century - with enough trees sprouting back to cover an area larger than England - that it has

to reverse from around the 1920s as more people began to move into cities, leaving marginal land to become populated again with trees. The US government, meanwhile, embarked upon an aggressive tree-planting program, with these factors leading to about 15m hectares of reforested area in the past century in the eastern US.



People work to reforest Allegheny National Forest in Pennsylvania circa 1934. Photograph: Universal History Archive/Universal Images Group via Getty Images

The recovery of the US's eastern forests has blunted global heating mainly through the trees' transpiration, in which water is drawn up through the roots to the leaves and then released into the air as vapor, slightly cooling the surrounding area.

By poring over data from satellites and weather stations located across the eastern US from 1900 to 2000, Barnes and her colleagues found reforested areas have provided this cooling impact on a grand scale, with most of this effect occurring within 400 meters of the trees.

In all, the replenished forests today cool the eastern US by 1C to 2C (1.8F to 3.6F) each year. The cooling effect is strongest on the hottest days in summer, when trees lower temperatures by 2C to 5C (3.6F to 9F), the researchers found.

The researchers cautioned that bringing back trees hasn't been the sole cause of the stalled warming, with factors such as airborne pollutants, which block incoming sunlight, and agricultural irrigation also potential causes. But Barnes said that the findings should further bolster efforts to provide thoughtful reforestation, particularly near urban communities that suffer particularly scorching temperatures due to a lack of shady trees.

"Trees have a really beneficial impact upon surface temperatures through transpiration, which is similar to human sweating, and they have really cooled things off a lot," said Barnes.



📷 Civilian Conservation Corps workers plant 15,000,000 trees across the wastelands of southern Mississippi on 11 April 1940. They are part of the United Forest Service which will re-establish forests destroyed by logging and lumbering operations decades ago. Photograph: AP

"Moving forward, we need to think about tree planting not just as a way to absorb carbon dioxide but also the cooling effects in adapting for climate change, to help cities be resilient against these very hot temperatures."

Patrick Gonzalez, a University of California, Berkeley, climate change scientist and forest ecologist who wasn't involved in the new study, said the work provides "strong support" to the theory of cooling trees.

"Cutting carbon pollution from cars, power plants and other human sources that burn coal, oil and methane remains the essential solution to halt climate change," he said. "Natural regeneration of trees and reforestation, where ecologically appropriate, can contribute substantially."

Barnes, too, stressed that reforestation was no substitute for the need to drastically cut planet-heating emissions, which hit a new global high last year.

"Nature-based climate solutions like tree planting won't get us out of this climate change problem," she said. "If anyone thinks we can just plant a few trees and be OK, they are wrong - we need a massive reduction in fossil fuel emissions to hit our targets. Reforestation is something that needs to happen in addition to, not instead of, cutting emissions."

I hope you appreciated this article. Before you move on, I wanted to ask if you would consider supporting the Guardian's journalism as we enter one of the most consequential news cycles of our lifetimes in 2024.

With the potential of another Trump presidency looming, there are countless angles to cover around this year's election - and we'll be there to shed light on each new development, with explainers, key takeaways and analysis of what it means for America, democracy and the world.

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And we avoid the trap that befalls much US media: the tendency, born of a desire to please all sides, to engage in false equivalence in the name of neutrality. We always strive to be fair. But sometimes that means calling out the lies of powerful people and institutions - and making clear how misinformation and demagoguery can damage democracy.



Effects of compound disturbance on Canada lynx and snowshoe hare: Wildfire and forest management influence timing and intensity of use

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Multi-objective management

ABSTRACT

Wildfires are increasing in scale and impact on the landscape, altering large amounts of wildlife habitat and forest ecosystems. The reduction of fuels through forest management is considered a primary way to reduce the extent and severity of wildfires before they occur but may lead to a decrease in tree density prohibitive of some species' habitat. Alternatively, management actions undertaken after a fire may speed the trajectory of burned areas back into quality habitat but may also impede this development if the wrong type of treatment is undertaken. Thus, information on how different management actions, applied either pre- or post-fire, can influence the timing of a burned area's return to suitable habitat will help managers conserve species on the landscape. Our study aims to understand how a rare carnivore, Canada lynx (*Lynx canadensis*), uses stands managed with different silviculture actions at different times relative to wildfire. We used GPS locations from 39 individual lynx collected from 2004 to 2015 to examine the response of lynx to wildfire compounded by active forest management, where time since fire at time of use ranged from 1 to 27 years. To understand the drivers behind lynx use of wildfires, we also focused on the primary prey of Canada lynx, snowshoe hares (*Lepus americanus*), using pellet counts across a similar range of post-fire treatment types in fires between 22 and 28 years old. We also assessed vegetation recovery and forest structure over time since wildfire using remotely sensed data and field measurements. We found that lynx intensity of use differed based on timing and type of management action, with the greatest lynx use ~25 years after a wildfire managed with post-fire regeneration cuts (removal of the majority of the canopy). Lynx use was likely driven by hare abundance, which was also highest in post-fire regeneration cuts, characterized at time of use by dense lodgepole pine stands. We conclude that managing landscapes with a mosaic of active (pre- and post-fire treatments) and passive (hands-off) management will best conserve a desirable range of lynx habitat in an increasingly fire-impacted landscape.

1. Introduction

Wildfire is one of the largest sources of habitat disturbance in forested ecosystems at a global scale (Curtis et al., 2018), and the continued effects of a warming climate and increased area of wildland urban interface, which can lead to increased human-caused ignitions and greater fuel availability through land-use change and fire-suppression around habitations (Pausas and Keeley, 2021; Radeloff et al., 2018), will only increase its impact. Decades of fire suppression and forest management decisions have led to changes in forest species composition, structure, and fuel loads, and combined with the effects of

a warming climate result in forests that may not be able to withstand the severity, extent, and frequency of contemporary wildfire disturbances (Stephens and Ruth, 2005). This increase in wildfire severity and frequency (Pausas and Keeley, 2021; Shvidenko and Schepaschenko, 2013; Williams et al., 2019) has rendered forests that were once ecologically resilient to fire susceptible to large-scale homogenization, such as through stand replacement of subalpine species with lower elevation heat tolerant species (Cassell et al., 2019), or permanent type conversion to non-forested ecosystems (Coop et al., 2020). This, in turn, may have cascading negative effects on some wildlife habitat (Driscoll et al., 2021), forest ecosystem services (Harris et al., 2021; Vukomanovic and

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HL Range: 50-60% mature) 14
20% adv regen

Holbrook = 33 km² = 8128

- use smaller stands - 14
avg HR = 26.5 m² = 16,960 ac. - up to 17,024
Hare HR = 7.5 → 25 ac

Driscoll et al. 2021 - 17,024

(69 km²)

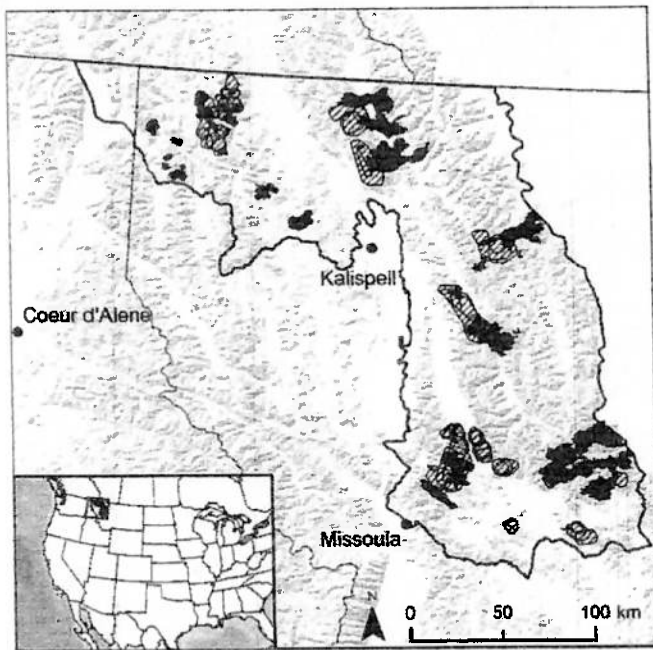


Fig. 1. The location of fires (red; $n = 25$) from 1988 to 2015 included in our study that overlapped with Canada lynx 95 % minimum convex polygon home ranges (black cross-hatching, $n = 69$) and hare pellet plots (blue dots, $n = 178$ plots) within the distribution of lynx (black outline) in the northern Rocky Mountains in western Montana, USA. Inset shows the location of the study polygon within the western United States. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Steelman, 2019), and human habitations and structures (Radeloff et al., 2018). Thus, there is a current strong motivation to apply forest management practices at large spatial scales to reduce fire extent and severity.

Extensive fuel reduction treatments are currently proposed for the western United States, with a plan by the United States Forest Service to treat up to 20 million acres on National Forest lands and 30 million acres across all other ownerships over the next 10 years (Wildfire Crisis Strategy, 2022). Forest management treatments mediate fire through the removal or redistribution of forest fuels, including live trees, standing dead, downed woody material, and shrubs or undergrowth (Stephens et al., 2012). A common management practice to reduce fire extent and severity is reduction of fuels using mechanical removal or prescribed burning to decrease tree densities and surface fuels before a wildfire takes place (Agee and Skinner, 2005; Stephens et al., 2021). However, fuels reduction can have deleterious effects on wildlife, especially those species that require dense or structurally complex forest. California spotted owls (*Strix occidentalis*; Tempel et al., 2014) and fisher (*Pekania pennanti*; Truex and Zielinski, 2013) both exhibit short term negative effects to fuel reduction treatments, although evidence indicates that these effects ameliorate over time and may be less destructive than high severity fire. Management actions chosen specifically to protect habitat can also mitigate negative effects on wildlife; for example, thinning by removing only small trees and removing debris from around specific nesting trees before a prescribed burn were both successful in mitigating fisher habitat destruction while decreasing fuels (Truex and Zielinski, 2013). These fine-scale pre-fire actions are time-consuming and difficult, however, and will thus be prohibitively expensive to impose at large spatial scales.

Once an area has experienced a wildfire, post-fire management actions are often carried out to attempt to speed landscape recovery or recoup financial losses through the harvest of remaining marketable timber. Similar to pre-fire management, post-fire actions shape the

trajectory of vegetation recovery and thus the temporal and spatial response of wildlife to burned areas (Jones et al., 2020; Kelly and Hodges, 2020; Nappi et al., 2004). Common post-fire management practices include removal of all or the majority of the canopy (clear-cutting) to reduce remaining fuels and regenerate a new cohort of trees, removal of large or marketable trees without emphasis on regeneration (salvage logging), or remedial actions such as planting or erosion control (Beschta et al., 2004). These different types of management actions differentially impact the amount and distribution of remaining vegetation, and thus impact wildlife habitat in turn. In addition, the spatial extent and arrangement of management actions is also important. Smaller, more heterogeneous actions may favor species that forage among edges or require dense cover, while larger patches, specifically those resulting from severe management actions, may be avoided by some species of wildlife (Smith, 2021; Squires et al., 2013). Current management drivers are such that the desire to reduce fuels over extremely large areas and to salvage timber in recent megafires are preeminent objectives, while the costs of these potentially compounding disturbances to wildlife communities is not well understood.

Subalpine forest species that rely on dense forest, mature trees, and complex forest structure are likely to be particularly impacted by both wildfire and widespread, simplifying forest management to mitigate wildfire. The subalpine forest ecosystem, composed primarily of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) at mid-elevations in the western United States (Agee, 1999) is experiencing increased burned area and fire frequency due to increased temperature and decreased precipitation (Higuera et al., 2021). Species such as fisher, spotted owls, and Canada lynx (*Lynx canadensis*) are known to depend on specific structural components related to mature and old-growth forests, elements which are lost through both severe wildfire and simplifying forest management. Here, we focus on Canada lynx, a threatened forest carnivore whose habitat is characterized by mature forest, high horizontal cover (dense cover of vegetation resulting from horizontal vegetation elements, such as tree boughs, saplings, and shrubs), and multi-storied vegetation that supports snowshoe hares (*Lepus americanus*), their primary prey (Holbrook et al., 2017; Ivan and Shenk, 2016; Squires et al., 2010). Lynx in the western United States are negatively affected at an immediate and often multi-decadal temporal scale by forest management actions such as clearcuts (removal of all trees) or selection cuts (patchy removal of some trees) (Holbrook et al., 2018), but less is known about their response to burned areas, especially in conjunction with forest management. Snowshoe hares avoid burned areas immediately after wildfire (although some use may take place within two years after the burn, with the return of understory vegetation [Keith and Surrendi, 1971]), but increase their use as shrub cover, dense young trees, and understory cover increase, generally 20–30 years post-fire (Cheng et al., 2015). Hare habitat is negatively impacted by forest management actions which remove understory and decrease tree density (Ferron et al., 1998; Griffin and Mills, 2007). Post-fire, hares were shown to avoid salvage logged areas (Keliv and Hodges, 2020) which removes remaining live trees and horizontal cover after a burn.

The goal of this work was to understand how the compound disturbances of forest management and wildfire influenced the timing and intensity of lynx use of burned areas. Previous research has shown lynx to use stands approximately 20–40 years after forest management, depending on the intensity of the harvest (Holbrook et al., 2018), and to use burned areas more if severity was low or date of fire older than 20 years (Vanbianchi et al., 2017b). The compound effect of forest management combined with wildfire is not well understood. To address this issue, we used GPS locations collected from 39 individual lynx in western Montana, USA from 2004 to 2015 combined with spatial data from 25 wildfires and 900 forest management stands. We also performed an evaluation of snowshoe hare abundance across various post-fire management actions in the same study areas. Since snowshoe hares are the primary prey of Canada lynx, this second data source

complements our analysis of lynx use of fires by providing information on the prey mechanism behind the observed patterns of lynx use. We evaluated the following primary hypotheses in our work: 1) the timing of forest management with regard to wildfire (i.e., management before versus after a fire) will alter lynx use intensity, with pre-fire management leading to lower severity fire and increased lynx use after a burn, and 2) less severe management action types (i.e., those that remove fewer trees) combined with wildfire will become useable more quickly for hares and lynx. To further explain lynx and hare response to the combination of fire and management, we investigated whether a suite of other fire-related characteristics influenced the timing and intensity of lynx and hare use of burned areas. Finally, we evaluated remotely sensed indices of forest vegetation recovery and forest structure to characterize forest vegetation conditions as they relate to management type and timing.

2. Methods

2.1. Study area

Our study area was located in the northern Rocky Mountains of northwestern Montana, USA, covering approximately 36,000 km² and delineated by previously estimated boundaries of current lynx distribution, as described in Squires et al. (2013; Fig. 1). Elevation within the study area ranges from 550 to 3400 m and climate is characterized by cold snowy winters and warm dry summers. Lynx habitat in this area is predominantly subalpine and mixed coniferous forest, composed of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) at drier low elevations and Engelmann spruce, western larch (*Larix occidentalis*), subalpine fir, and lodgepole pine at higher, more mesic elevations. Land use in our study area is primarily (~80 %) federally owned multiple use public land, which allows management for timber harvest, recreation, water and wildlife conservation, and grazing (Multiple-Use Sustained-Yield Act of 1960) plus some private and state-owned land. Much of observed lynx habitat in the northwestern Rocky Mountains historically had mixed severity fire regimes, with an estimated 20 % of forested area burned in stand-replacement fire, 30 % in nonlethal severity, and 50 % in mixed severity (Arno et al., 2000). For the past several decades, however, fires have occurred on the landscape with increasing frequency, size, and severity (Jolly et al., 2015; Salguero et al., 2020), with an estimated increase of 889 % in the number of wildfires and 2966 % in the amount of burned area from 1973 to 2012 on public lands in the Northern Rocky Mountains (Westerling, 2016).

3. Lynx locations

Our lynx dataset was initially composed of 69 adult individuals collared in western Montana, USA, from 2004 to 2015. Of these, 39 individuals (17 females and 22 males) had home ranges that overlapped with wildfires, resulting in 17,660 GPS locations considered for our analysis (individual distribution across years, some animals collared in multiple years: 2004 n = 1, 2005 n = 8, 2006 n = 8, 2007 n = 5, 2009 n = 1, 2010 n = 2, 2011 n = 4, 2012 n = 8, 2013 n = 9, 2014 n = 2, 2015 n = 3). All lynx were live-trapped using specially designed box-traps (Kolbe et al., 2003) and fitted with store-on-board GPS collars (Lotek Wireless, Newmarket, Ontario, Canada or Sirtrack Ltd., Havelock North, New Zealand) weighing < 3 % of lynx bodyweight. Lynx capture and handling methods were approved under University of Montana IACUC permits 4-2008 and TE053737-1. Lynx were primarily captured in January through March, with GPS collars programmed to collect one location every 30 min for 24 h on alternate days until the programmed drop-off date. On average, collars collected a mean of 129 days (range: 4–362) of data, and a mean of 2342 locations (range: 44–7626) during this time, with an average fix success of 86 %.

4. Lynx response to management type and timing

We defined the spatial extent of our analysis as the intersection of lynx home ranges, wildfires, and forest management actions, with the management polygon (or stand) as our individual sample unit. To estimate lynx home ranges, we used 95 % minimum convex polygons (MCP) for each lynx (n = 39) from 2004 to 2015; home ranges averaged 69 km² (range: 13–330 km²). We used the MTBS (Monitoring Trends in Burn Severity; MTBS Project, 2015) dataset to determine the extent and severity of wildfires that overlapped with lynx home ranges within our study area; we included 25 fires from 1988 (the oldest fire in the MTBS dataset to overlap a lynx home range) to 2015 (to coincide with our most recent year of lynx locations); fires were 1 to 27 years old at the time of lynx use. To determine spatially co-occurring management actions, we used the FACTS (Forest Activity Tracking System) database, which is compiled by the U.S. Forest Service (USFS) and records the type and date of management action that took place (spatially limited to USFS land ownership and temporally spanning ~ 1960 to present), as well as the shape and location of the stand in which they occurred. For all analyses, we used this stand-based approach, with dependent and independent variables summarized to a given FACTS-based polygon.

For our study area, the FACTS database contained 48 unique categories of management actions that we determined would influence vegetation in some way. Previously, Holbrook et al. (2018) examined the response of Canada lynx in our study population to forest vegetation management, and developed a classification of management actions into categories based on a strong and differential signature of NBR (normalized burn ratio) across time that indicated variation in severity of vegetation removal and thus also of post-management vegetation recovery. The NBR correlates strongly with overstory and understory vegetation covariates, such as percent canopy cover (Hudak et al., 2004) and has been shown to reflect long-term vegetation recovery after a burn (Chen et al., 2011). Therefore, we adopted this same categorization, which classifies vegetation altering management actions depending on the severity of vegetation removal, into "Thinning", "Selection Cut", and "Regeneration Cut", from least to most severe, respectively (see Appendix A for the classification of all actions). In addition, we added the categories "Salvage Cut" and "Planting", as these were unique management actions that were associated with fires but were not represented in Holbrook et al. (2018). In general, Thinning treatments reflected partial canopy removal, generally of small trees ~ 15 cm, to improve stand growth; Selection Cut treatments included removal of overstory or competing trees to release remaining trees from competition; Regeneration Cut treatments were even-aged regeneration harvests such as clearcuts that removed all or most of the canopy; Salvage Cut treatments removed marketable timber after fire or insect loss without emphasizing regeneration; and Planting treatments were actions that introduced artificial regeneration.

We limited our dataset of management stands to post-fire actions ≤ 10 yrs after a fire and pre-fire actions ≤ 25 yrs before a fire, since we reasoned that actions that occurred > 10 yrs after a fire were increasingly unrelated to the original fire conditions, and actions that occurred > 25 yrs before a fire were old enough at the time of fire to be difficult to distinguish from unmanaged stands. Furthermore, we did not include stands with management both before and after a fire, which would confound our pre- versus post-treatment analysis. We also included stands where no active management occurred to serve as a comparison group. This resulted in a total of n = 900 stands for analysis. For each unique FACTS polygon, our initial thought was to assign a single management category to represent the management that had occurred there. As we assembled the dataset, however, we realized that many stands had multiple actions which occurred over a span of decades, and that these combinations would make the effects of individual management categories difficult to interpret. Therefore, we created a second, limited dataset with which to examine the effects of management category, since limiting FACTS polygons to one or two management categories

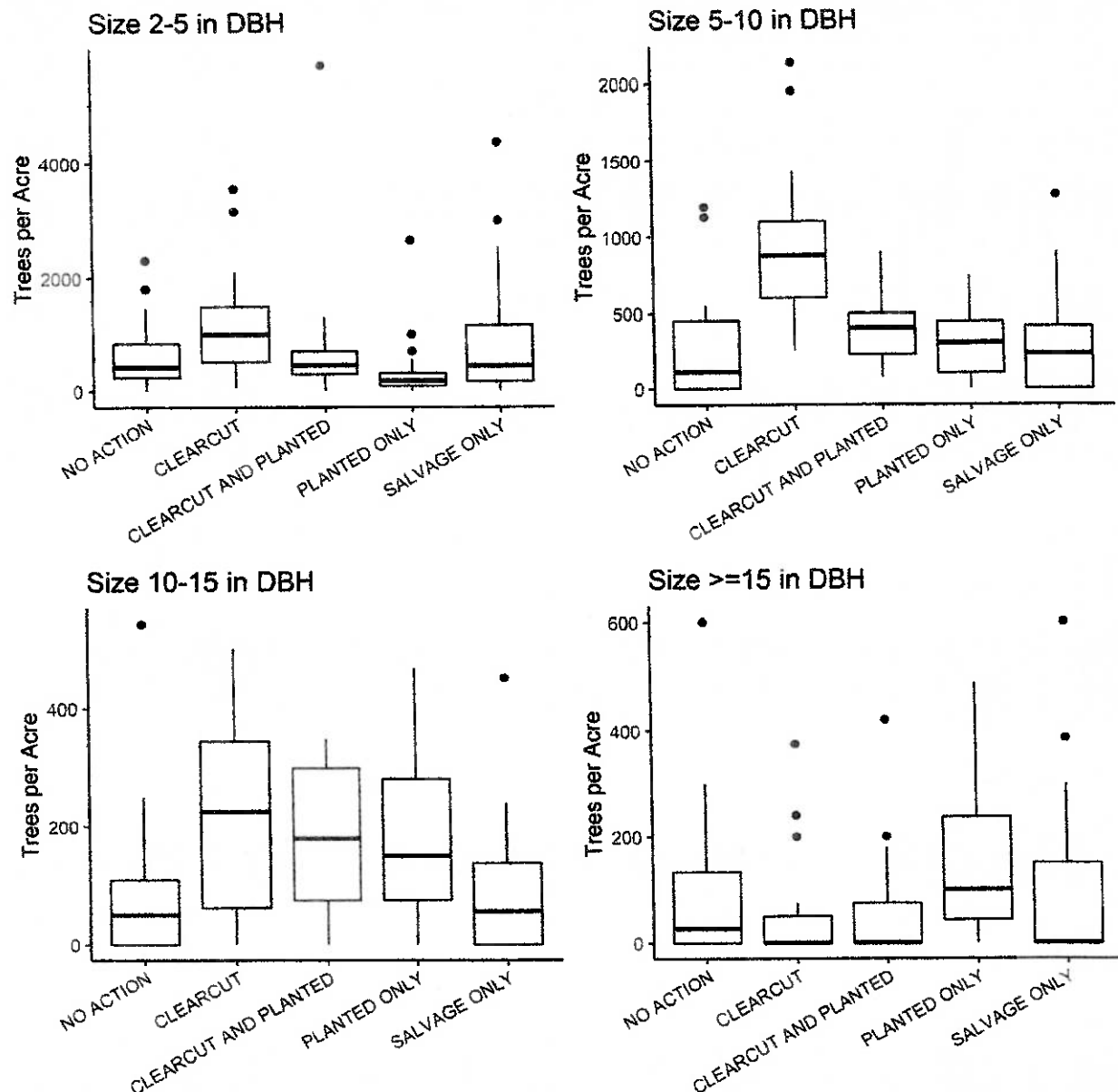


Fig. C2. Boxplots of four size classes of trees (5.1–12.7 cm [2–5 in], 12.7–25.4 cm [5–10 in], 25.4–38.1 cm [10–15 in], ≥ 38.1 cm [≥ 15 in]) sampled at hare pellet plot locations across various categories of post-fire management actions in 22–28 year old fires in western Montana, 2015 and 2016. The 'Clearcut' category has greater median trees per acre for all size classes < 38.1 cm [15 in] DBH.

Murray, 2002) and to select mid-successional forest with dense stem counts, with high use generally 20–30 years after disturbance: hares were most numerous 15–40 years after disturbance in Idaho (Thornton et al., 2012), 17 years after fire in Montana (Cheng et al., 2015), and 20 years after disturbance in Washington (Koehler, 1990). In the Alaskan taiga, Canada lynx and snowshoe hares both showed a preference for 25–28 year old burns, in forests with ~ 9000 saplings/ha and 900 live trees/ha (Paragi et al., 1997). A caveat to our results, however, is our small sample size, particularly for pre-fire management actions. Stands in our study area tended to be subject to multiple forest management actions over time; to avoid confounding different silvicultural actions, we did not include stands with more than two management categories, which severely limited our sample size and thus our ability to detect patterns in lynx use relative to pre-fire management type over time. Furthermore, lynx response to pre-fire management actions may be mediated by disturbance to the understory, with treatments that preserve understory trees likely to favor faster recovery of snowshoe hare

and lynx habitat (Squires et al., 2020; Sullivan et al., 2010). Anecdotally, we have observed stands in our study area that were treated pre-fire with a management action that removed small understory trees and were then generally avoided by lynx due to low horizontal cover for more than two decades post-treatment. Thus, while our results did not detect a difference in lynx use depending on the type of pre-fire management action, we recommend that managers consider the importance of the understory to lynx and hares when planning large fuel removal treatments.

Fire severity was also an important factor in lynx use of previously burned areas: lynx used high severity fire less over time compared to non-burned areas. Severity is a key factor influencing the impact of wildfire on wildlife habitat. Marten (*Martes caurina*) and lynx have been shown to select sites with lower burn severity 1–13 years after fires in Washington and British Columbia (Volkman, 2021; Volkman and Hodges, 2022), while spotted owls (Jones et al., 2020) and bighorn sheep (*Ovis canadensis canadensis*; Donovan et al., 2021) were shown to

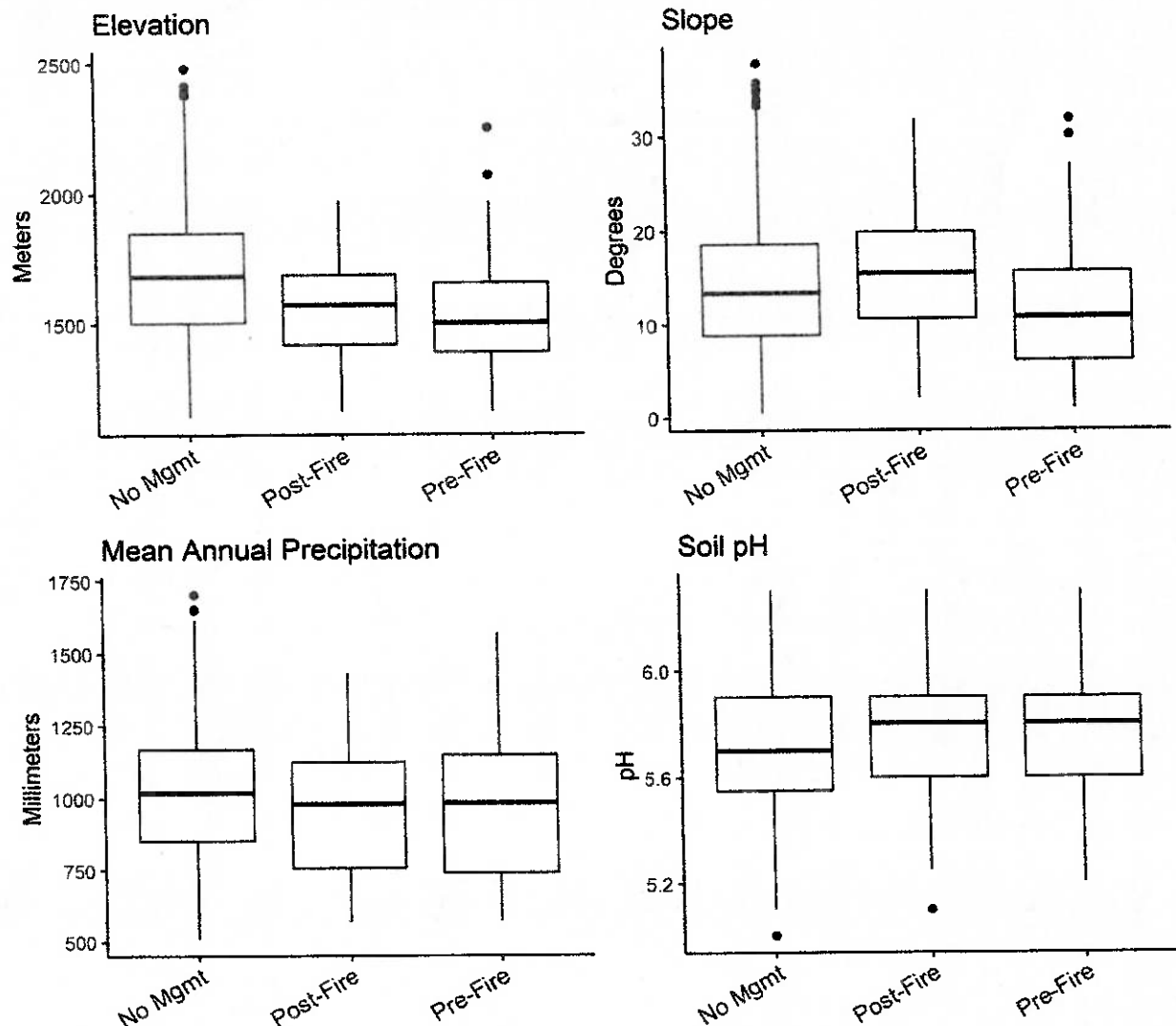


Fig. D1. Boxplots showing differences in elevation, slope, mean annual precipitation, and soil pH for burned stands that have no active management, post-fire, or pre-fire management within the distribution of Canada lynx in western Montana.

select severely burned areas, provided that sufficient heterogeneity in fire severity was present. Vanbianchi et al. (2017b) found that lynx in Washington were more likely to use low severity burned areas or unburned vegetation within burns and emphasized the importance of maintaining any remaining live trees inside fires to provide hare habitat. Our work agrees with these results and stresses the importance of maintaining forest heterogeneity when implementing forest management actions to both mitigate wildfire and conserve lynx. While lynx responded positively to regeneration cuts implemented post-fire, use was lower than stands that received no management or pre-fire management for approximately 10–15 years. Thus, while this type of management is likely to lead to good lynx habitat in ~ 25 years, stands that are not actively managed or that were managed before the fire are also required to provide useable post-burn habitat immediately and in the short-term after a fire. Previous work on this (Holbrook et al., 2019) and other populations of lynx (Ivan and Shenk, 2016; Kochler and Brittelli, 1990; Vanbianchi et al., 2017a) have also demonstrated the importance of maintaining a mosaic of forest structure classes within a lynx home range, with the greatest reproductive success of lynx in our study area found when a home range is composed of ~ 50–60 % mature and ~ 20 % advanced regeneration (Holbrook et al., 2019). Lynx in our study also showed some response to the size and shape of managed stands, with greater use of small or more complex shapes in both managed and non-

managed stands, indicating further support for a heterogeneous mosaic of forest patches.

Differences in hare relative abundance also highlighted the importance of a managed landscape mosaic, showing the most predictive characteristics were related to the 4 km landscape around a given stand. Hares were more abundant in salvaged or non-managed stands when a high proportion of management was in the surrounding neighborhood. Our investigation into forest structure relative to wildfire indicated that managed stands had a greater proportion of advanced regeneration lodgepole pine forest that hares prefer. Thus, we may see higher abundance of hares in non-managed stands in this case because surrounding stands have high hare abundance. Lewis et al. (2011) found a similar response to neighboring conditions in hares in Washington, with more hares in patches surrounded by high quality habitat.

An unexpected result of this work was the slower trajectory of vegetation recovery and the low lynx and hare use of non-managed burned areas. We initially expected that vegetation removal through forest management, particularly post-fire management, would compound the wildfire disturbance and result in longer time to use and lower quality of lynx habitat. Instead of a compounding effect, we found an opposite disturbance mitigating effect, with non-managed stands showing the slowest NBR recovery and both pre- and post-fire managed areas used more intensively by lynx over time. We found no evidence to

☆ - use smaller ☆

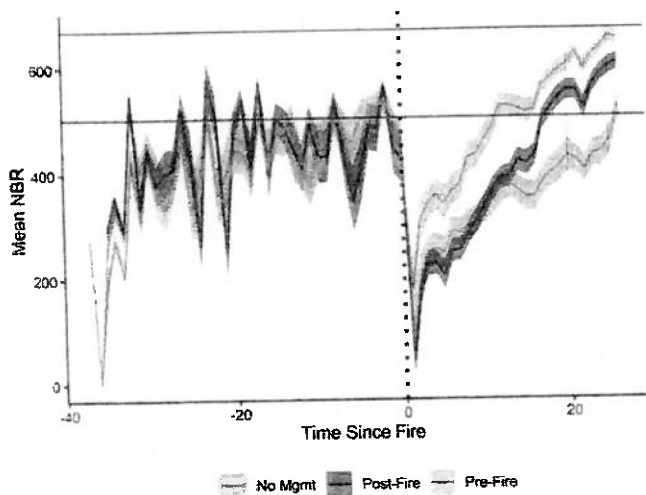


Fig. D2. The average ($\pm 90\%$ confidence interval) vegetation trajectory before and after a wildfire in stands that have active or passive management within lynx distribution in the northern Rocky Mountains, Montana. The colors represent when management occurred relative to the wildfire, solid black horizontal lines indicate the range of NBR values in unburned lynx home ranges, and dotted vertical line indicates the year that wildfire occurred. This plot demonstrates that before the wildfire, all stands in our analysis followed a relatively level NBR trajectory with some stochasticity between years, but after a wildfire, these trajectories differed significantly based on the timing of active management in the stand.

indicate that differences in accessibility or growing conditions existed between managed and non-managed stands (see Appendix D for details), thus, one possible reason for this is our result that more non-managed stands burned at high severity than those with pre-fire management. High severity fire in subalpine forests can result in decreased ground cover and shrub cover a decade or more after a fire (Turner et al., 2003), as well as high tree mortality (Hood et al., 2018) and reduced tree regeneration (Hansen et al., 2018; Turner et al., 2019), contributing to slow vegetation recovery. Furthermore, increasingly warm temperatures and greater drought caused by global climate change are contributing to greater fire severity, particularly in forests in the western United States, which may lead to a loss of lynx habitat through a change from mesic higher elevation subalpine species to species tolerant of hot and dry conditions (Cassell et al., 2019), or a conversion to non-forest (Coop et al., 2020). However, our results also showed that non-altered stands maintained more mature forest structure immediately after a burn than stands that had been silviculturally managed either pre- or post-fire, and Vanbianchi et al. (2017b) confirm the importance of non-managed areas to lynx in recent fires. Mature forest is an important element of lynx habitat, particularly in the winter (Ivan and Shenk, 2016; Squires et al., 2010), providing consistent forage and cover for hares. The presence of mature forest has also been shown to relate to reproductive success of female lynx in our study population, with the most successful females maintaining core home ranges with $\sim 60\%$ mature forest in large, connected patches (Holbrook et al., 2019;

Kosterman et al., 2018). Moreover, while we found that pre-fire management did reduce the proportion of stands that burned at high severity, these stands also had less mature forest structure and more sparse forest after a fire, indicating that pre-fire management is not a panacea for lynx habitat. Therefore, while passively managed stands may be slower to provide lynx habitat after a wildfire, they still play an important role in the forest mosaic needed to support lynx.

11. Conclusions

This work illuminated the importance of the timing of forest management with respect to wildfire, highlighted the role of spatial and temporal scale when considering management mosaics on the landscape, and suggested bottom-up processes underlying carnivore behavior in the face of large-scale compound disturbances. The conservation of lynx habitat given the challenge of large and severe wildfires depends on the maintenance of stand heterogeneity through a thoughtful management approach that includes pre- and post-fire treatments, while keeping in mind that most silvicultural treatments will render the area unfavorable to lynx for at least the next 10 years. Thus, a mosaic of active and passive managed stands in different age classes is important at the home range scale, which for lynx in our study area has averaged between 33 km^2 (Holbrook et al., 2019) to 69 km^2 (this study). Within a home range, female lynx had between 0 and 16 % of their entire home range in stand initiation (Holbrook et al., 2019); based on our analysis, we found 30–70 % of the managed and non-managed stands in our study reverted to stand initiation immediately after a wildfire (Fig. 5), illustrating the difficulty that managers face in maintaining acceptable levels of non-favorable structure classes at the home range scale when fires are large. At the temporal scale, our work speaks to the importance of temporal connectedness among land managers, given that the benefits of treatments for hares and lynx will be realized over the course of an entire career for most people ($\sim 25\text{--}30$ years). Therefore, ensuring current management decisions consider the actions of both past and future managers will be essential to fully embrace the spatio-temporal detail underlying the patterns we uncovered with Canada lynx and snowshoe hares.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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We would like to thank the many hard-working field personnel who fought through thickets of lodgepole to collect this data. We thank S. Baggett for providing statistical advice and two anonymous reviewers for thoughtful comments that improved the manuscript. We also acknowledge the U.S. Department of Agriculture, U.S. Forest Service, Region 1 for their financial support of this work.

Appendix A

The list of U.S. Forest Service FACTS database activity classes and the management category into which they were grouped for analysis. Categories correspond to those used in Holbrook et al. (2018).

Science

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"Science affects the way we think together." *N. Parks-*
Lewis Thomas

ON THE TRACK OF THE ELUSIVE WOLVERINE



John Rohrer

Snow cover that lingers into May is a defining habitat feature for wolverines in the contiguous United States.

"Picture a weasel—and most of us can do that, for we have met that little demon of destruction, that small atom of insensate courage, that symbol of slaughter, sleeplessness, and tireless, incredible activity—picture that scrap of demoniac fury, multiply that mite some fifty times, and you have the likeness of a Wolverine."

—Ernest Thompson Seton

The wolverine has a near-mythical reputation. Stories abound of wolverines chasing down or leaping on the backs of animals as large as moose, harassing bears and wolves over prey, ravaging hunters' cabins, and even

attacking humans. However, most of these stories are either misunderstandings of wolverine behavior or tall tales. Although there have undoubtedly been altercations between wolverines and bears or wolves over potential food sources, wolverines do not try to compete directly with these much larger predators—in fact, wolverines are primarily scavengers. Their long canine teeth and claws, a sense of smell so acute they can sniff out animals buried under 6 feet of snow, and muscular jaws capable of breaking bone and tearing apart even frozen flesh—likely earned wolverines their scientific name: *Gulo gulo*, meaning "gluttonous glutton." Related to weasels and otters, wolverines resemble small bears with bushy tails, and the musky odor they exude has elicited such nicknames as "skunk-bear."

IN SUMMARY

The wolverine is one of the rarest and least-known mammals in North America. A lack of understanding regarding its historical distribution in the contiguous United States and its broad-scale habitat needs has hampered conservation efforts. Using a suite of research methods, including the assemblage of historical data on wolverine occurrence, analyses of habitat factors, GIS mapping, radio-telemetry tracking, and genetic studies, researchers were able to address these information gaps.

Their findings show that historically, wolverines occurred primarily in high-elevation areas of the major western mountain ranges and in the Great Lakes region, where spring snow cover persisted throughout the animals' reproductive denning period. By the mid-1900s, the wolverine's range was dramatically diminished, owing probably to high levels of human-caused mortality and low or nonexistent immigration rates.

Today, wolverines survive in high-elevation pockets of northern Washington, northwestern Montana, south-central Idaho, and northwestern Wyoming. Throughout the year, wolverines stay within areas characterized by persistent spring snow cover, even when dispersing to new locales, and avoid areas with warmer temperatures to prevent thermal stress. This narrowly defined "bioclimatic envelope" suggests the wolverine's range will retreat northward in the face of climate change, but it also offers an empirical basis for initiating new conservation efforts.

Given that *Gulo gulo* evolved in the Arctic, the researchers speculated that wolverines may remain in high-elevation areas during the snow-free summer months to avoid overheating at lower elevations. To examine this hypothesis, the researchers overlaid the telemetry points on a map depicting the areas where maximum summer temperatures were typically less than 72 °F. "Although prey availability and other habitat factors may also play a role," Aubry notes, "our analyses indicate that even after the snowpack has melted, wolverines continue to use the same areas they used during the winter due to an upper limit of thermal tolerance." Thus, the researchers concluded that persistent spring snow cover provides a reliable and spatially explicit model of the wolverine's "bioclimatic envelope" throughout its circumboreal range.



LAND MANAGEMENT IMPLICATIONS



- The wolverine's specialized habitat requirements, combined with rising temperatures owing to global climate change, make it highly likely that wolverine populations in the contiguous United States will become even more fragmented than previously recognized.
- The reestablishment of wolverine populations in California, Colorado, and Utah is unlikely to occur without human intervention. Because human activities such as trapping and poison-baiting no longer pose significant threats, reintroduction may be an appropriate management strategy.
- The strong body of scientific evidence demonstrating that wolverines are closely associated with areas that contain persistent spring snow cover offers a sound empirical basis for managing the habitat conditions that are most important to wolverines.

IMPLICATIONS OF GLOBAL CLIMATE CHANGE

These studies have yielded important new insights into the nature of the wolverine's ecological niche in North America. Unfortunately, recent findings don't bode well for the species' future as the planet—and particularly the Arctic—continues to warm. "The wolverine may be second only to the polar bear in its sensitivity to global warming," Aubry contends. "If current warming trends continue, the spring snow cover layer will shift upwards in elevation and shrink in geographic extent, increasing the fragmentation and isolation of wolverine habitat," he explains. "We believe our research provides an empirical basis for identifying the most likely areas of wolverine persistence in the face of global climate change, and the most significant habitat corridors for maintaining connectivity among their populations," he adds.

The findings have already been used in a policy analysis related to the species. The U.S. Fish and Wildlife Service (FWS) relied extensively on the researchers' distributional analysis in its 2008 review for potential listing of *Gulo gulo* under the Endangered Species Act. However, the FWS ruled that listing was not warranted because the wolverine population in the contiguous United States is connected to populations occurring in Canada, and does not represent a significant portion of wolverine range in North America.

Although *Gulo gulo* faces an uncertain future, the species can only benefit from this growing knowledge of its ecology. "The wolverine is an iconic symbol of the American wilderness,



Wolverine tracks.

Dan Russell

and if we can produce new scientific knowledge that contributes to understanding its habitat requirements in the lower 48, then we'll be helping to preserve a part of our heritage that has significant value to a great many people, whether or not they ever see a wolverine in the wild." Aubry declares.

"Man masters nature not by force but by understanding."

—Jacob Brownowski

FOR FURTHER READING:

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WRITER'S PROFILE

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RED SQUIRRELS IN THE WHITEBARK ZONE

Daniel P. Reinhart
David J. Mattson

90 ft/ae =
threshold

ABSTRACT

Reports results of a study of interactions among red squirrels (*Tamiasciurus hudsonicus*), bears (*Ursus* spp.), and whitebark pine (*Pinus albicaulis*) from 1984 through 1987 in north-central Yellowstone National Park and in the vicinity of Cooke City, MT. This paper deals with results that pertain to habitat relationships of red squirrels in the whitebark pine zone. Indices of red squirrel activity and abundance were highest in the mesic and wet habitat types. Pure whitebark pine stands were apparently not favorable habitat for red squirrels. In the whitebark pine zone, cones of other conifer species were needed to offset yearly variations in whitebark pine cone production. Optimal red squirrel habitat in this zone consisted of stands with high tree species diversity, basal area, and environmental favorability. Annual fluctuations in red squirrel densities reflected yearly whitebark pine cone production in stands with a high whitebark pine component. Bears may play a role in regulating red squirrel abundance in whitebark pine stands.

INTRODUCTION

Red squirrels (*Tamiasciurus hudsonicus*) are commonly associated with coniferous forests. They range extensively in the boreal regions of North America from Alaska to Arizona and from northern Quebec to the Appalachian Mountains (Smith 1970). Red squirrels are typically diurnal, solitary, and active throughout the year. Their diet consists primarily of the reproductive products of trees, fungi, and shrubs within the forests they occupy (C. Smith 1968). Although red squirrels are well adapted to live on a variety of foods available during the growing season (Ferron and others 1986), in the Rocky Mountains they must rely on stored conifer seeds for half the year (Finley 1969; Rusch and Reeder 1978). Conifer seed cones represent storable, high-energy packages that are relatively resistant to spoilage (Weigl and Hanson 1980).

Red squirrels subsist on a seasonal food supply on a year-round basis by caching and storing conifer seed cones gathered within established, defended territories. Gathering and storing cones occupy up to 80 percent

of their daily activity from August through November (C. Smith 1968). Individual territories are nonoverlapping and contiguous within forest habitats and are defended from other red squirrels regardless of sex by vocalizations and by chasing intruder squirrels (Rusch and Reeder 1978; C. Smith 1968).

A large, centralized midden is a major feature of a red squirrel territory. Middens are sites traditionally used to cache and feed on cones and consist of large amounts of cone clippings. They occasionally extend into springs, bogs, and creek bottoms where added moisture helps preserve cones in a closed, more storable condition (Finley 1969).

In high-elevation mountain forests of western North America, whitebark pine (*Pinus albicaulis*) trees produce annually fluctuating crops of large, edible seeds (Forcella and Weaver 1986). These seeds are extensively used by wildlife such as Clark's nutcracker (*Nucifraga columbiana*), bears (*Ursus* spp.), and red squirrels (Kendall 1981; Tomback 1982). The large, edible seeds of whitebark pine are apparently preferred over other conifers by red squirrels and are readily cached when available (Hutchins and Lanner 1982). Whitebark pine seeds are also an important fall and spring food for grizzly bears (*Ursus arctos*) within the Yellowstone ecosystem and are obtained almost exclusively by raiding squirrel caches (Kendall 1981). During 1984 through 1987 the Interagency Grizzly Bear Study Team (IGBST) studied the interrelationships of grizzly bears, red squirrels, and whitebark pine. Habitat relationships of red squirrels within the whitebark pine zone are presented here.

STUDY AREA

Our study area consisted of the Mount Washburn massif in north-central Yellowstone National Park, and an area in the Gallatin National Forest near Cooke City, MT (fig. 1). Both areas were located in higher elevations of the subalpine zone on moderately steep topography. Elevations ranged from 2,360 m (7,800 ft), just below the lower elevational limits of whitebark pine distribution, to 2,865 m (9,400 ft) at the upper limits of erect tree growth.

Most study area timber cover was mature to over-mature with some stands of pole-sized, even-aged trees. Whitebark pine occurred throughout the study area and was variously represented from dominant to scattered individuals. Whitebark pine was more prevalent in the Mount Washburn area than in the Cooke City area, where lodgepole pine (*Pinus contorta*) was a more common dominant.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 28-31, 1988.

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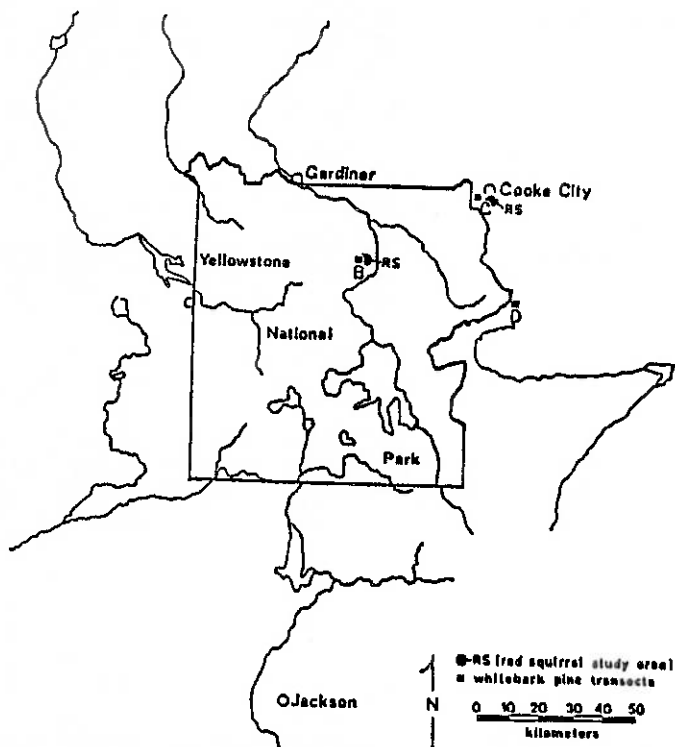


Figure 1—Location of red squirrel study areas (RS) and whitebark pine transects: Mount Washburn (B) and Cooke City (C).

The study area included five major habitat types described by Steele and others (1983). The *Pinus albicaulis* (PIAL) series habitat types prevailed at high elevations on west and south aspects. The *Abies lasiocarpa/Vaccinium scoparium*-*Pinus albicaulis* (ABLA/VASC-PIAL) and *Abies lasiocarpa/Vaccinium globulare-Vaccinium scoparium* (ABLA/VAGL-VASC) habitat type phases were the most common habitat types in our study area. The *Abies lasiocarpa/Vaccinium scoparium-Vaccinium scoparium* (ABLA/VASC-VASC) phase, *Abies lasiocarpa/Thalictrum occidentale* (ABLA/THOC), and *Abies lasiocarpa/Spiraea betulifolia* (ABLA/SPBE) habitat types occurred at low elevations. The wet site *Abies lasiocarpa/Calamagrostis canadensis* (ABLA/CACA) type was found near creek bottoms and seeps.

METHODS

We delineated homogeneous timber stands on USGS 15-ft topographic maps and 1:20,000 and 1:30,000 color aerial photographs. Line transects were laid out to intercept all stands so that no transects intersected and stand edge effect was minimized. Transects were laid out without bias toward timber stands or toward the monitored squirrel population. Transect lengths were determined from airphotos and corrected for slope.

Field work was conducted from mid-August to mid-September from 1984 through 1987. Beginning and end points were located using airphoto interpretation and marked with stakes. Two people walked all transects each year during daylight hours; one person maintained compass bearing and distance pacing, while the other person was responsible for observing and recording squirrel sign. Regular pauses were observed every 100 to 200 m in each stand for habitat evaluation.

All stands were identified by forest habitat type (Steele and others 1983) and forest cover type (Despain 1977; Mattson and Reinhart, this proceedings). In addition, between 5 and 26 systematically placed variable-radius overstory plots were taken in each stand (Mattson and Reinhart, this proceedings).

Red squirrel data were collected annually while walking line transects (Eberhardt 1978). Squirrel sign was referenced to transect locus and perpendicular distance from transect. All unduplicated sightings or vocalizations discerned from the transects and estimated to be within stand bounds were recorded. All individual squirrel middens observed from transects were noted and described as active or inactive based on the presence of cached cones, fresh cone clippings, or squirrels. Red squirrel activity was recorded between 0 to 60 m from transect lines. Bear activity and bear-excavated red squirrel middens were also noted.

We calculated two indices of relative squirrel abundance for habitat types and for habitat type-cover type combinations. We summed sightings and vocalizations and divided by total transect length to derive linear frequency of occurrence. Similarly, we divided total middens by transect length to derive linear frequency of middens.

Annual whitebark pine cone production for Cooke City and Mount Washburn study areas was obtained by counting cones on marked trees along predetermined whitebark pine cone transects (Blanchard, this proceedings).

RESULTS

Data were collected on up to 50 km of line transects per study year. Between 41 and 57 transects that sampled between 40 and 74 stands were walked annually on Mount Washburn. Between 15 and 22 transects surveyed between 51 and 65 stands near Cooke City.

Annual whitebark pine cone production varied widely in the study areas (fig. 2). Whitebark pine cone production was highest in 1985 and lowest in 1986. Cone crops in 1984 and 1987 were intermediate. Cooke City cone data were missing in 1984 and therefore extrapolated using simple linear-regression. Actual cone production in 1987 was believed to be higher than the cone counts indicated because of earlier than normal cone maturation and harvest and late cone surveys (Blanchard, this proceedings).

Several patterns were evident by linear counts of vocalizations plus sightings and active middens (table 1, fig. 3):

1. Relatively little squirrel activity occurred in PIAL series habitats on Mount Washburn. These were mostly pure near-climax whitebark pine stands.

2. Moderate amounts of squirrel sign were found on the drier ABLA/SPBE type and in the ABLA/VASC-PIAL phase.

3. A higher incidence of red squirrel activity occurred in more mesic habitats represented by the ABLA-THOC habitat type and the ABLA/VAGL-VASC and ABLA/VASC-VASC phases and in the wetter sites of the ABLA/CACA habitat type.

We calculated annual variation of squirrel density indices for the major study area habitat types (table 1). On Mount Washburn (fig. 3A), annual variation in squirrel abundance generally reflected annual variation in white-bark pine cone production. This pattern was most evident in the ABLA/VASC-PIAL phase but was also apparent in the other more mesic habitat types. At Cooke City (fig. 3B), sequential years' variation of squirrel densities was not as pronounced as on Mount Washburn with the exception of the ABLA/VASC-PIAL phase where variation did reflect the whitebark pine cone crop.

There were differences in the extent of variation among years between the two indices used to measure squirrel abundance (fig. 3). Linear densities of vocalizations and

Table 1—Mean densities (n/km) and coefficients of yearly variation of active red squirrel middens for habitat types of the two study areas

Habitat type	Midden density			
	Mount Washburn		Cooke City	
	$\bar{X}$	C.V.	$\bar{X}$	C.V.
ABLA/CACA	3.64	0.506	2.35	0.719
ABLA/THOC	3.20	0.233	1.63	0.355
ALBA/VAGL-VASC	2.60	0.079	1.92	0.250
ABLA/VASC-VASC	2.78	0.243	—	—
ABLA/VASC-PIAL, LP cover type	3.80	0.389	4.34	0.737
ABLA/VASC-PIAL, WB cover type	1.15	0.548	1.38	0.188
ABLA/SPBE	1.53	0.580	—	—
PIAL series	0.11	0.200	—	—

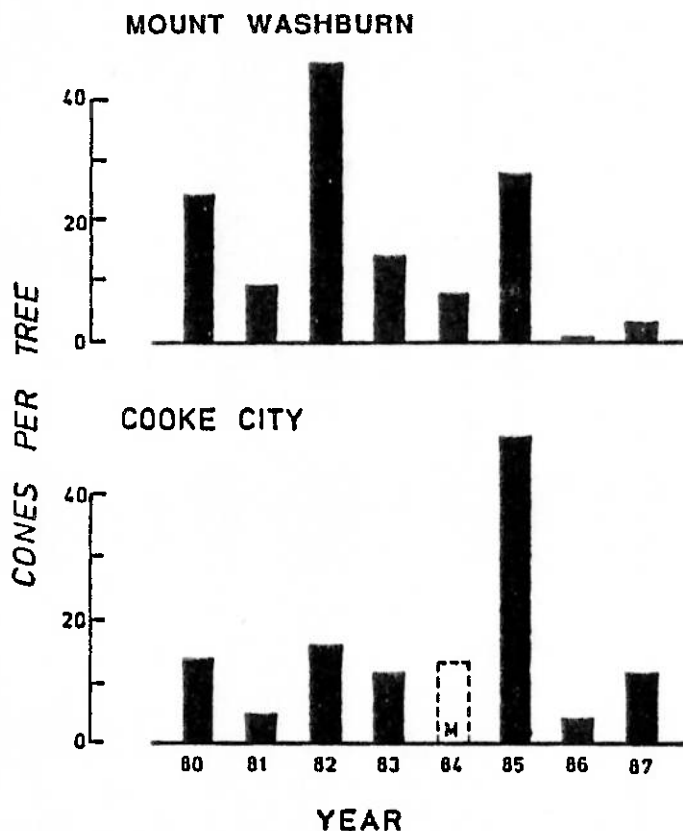
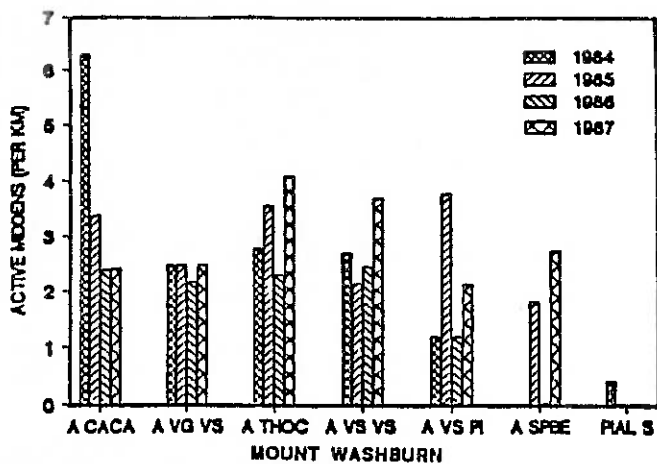


Figure 2—Whitebark pine cone production, 1980-1987, for the Mount Washburn and Cooke City study areas. Cone production for Cooke City in 1984 was extrapolated.

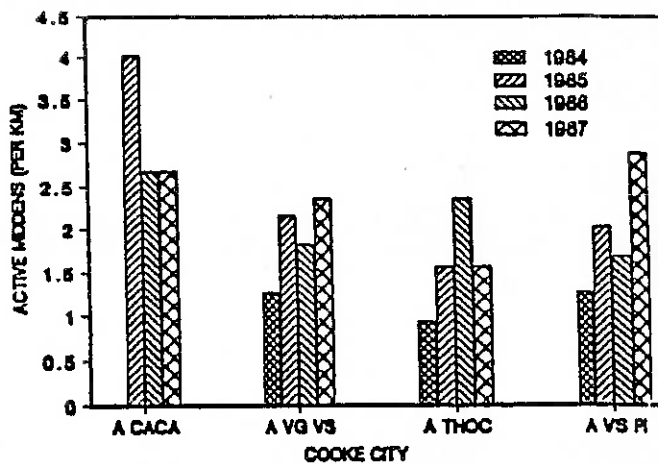
sightings varied more than linear densities of active middens. There was also an exponential increase in the density of vocalizations plus sightings relative to the increase in the density of active middens ($r^2 = 0.959$, $P < 0.001$) (fig. 4).

Average linear frequency of middens for different habitat types was positively related to average timber basal area ($r^2 = 0.675$, $P < 0.001$) (fig. 5). The ABLA/VASC-PIAL habitat type-whitebark pine cover type deviated the most from this relationship. Lodgepole pine cover types of the ABLA/VASC-PIAL phase fit the general relationship of basal area and squirrel density. At an average basal area of less than $67.7 \text{ m}^2/\text{ha}$ ($90 \text{ ft}^2/\text{acre}$), no resident squirrels occurred. Mean basal area for the PIAL series defined this extreme end point.

We also related a synthetic environmental variable, "site favorability," to mean squirrel midden abundance (fig. 6). Site favorability was an index that positively weighted direct solar radiation and negatively weighted wind exposure and elevation. Mattson and Reinhart (this proceedings) more fully described this variable. Squirrel abundance was lowest on the coldest, highest, and most wind-exposed habitat types ($r^2 = 0.792$, $P < 0.001$). Variation from this relationship was associated with overstory species diversity and higher basal areas of whitebark pine and Douglas-fir (*Pseudotsuga menziesii*). Habitat types with less squirrel densities included the PIAL series, which consisted of almost pure whitebark pine stands, and the ABLA/VASC-VASC phase, which consisted of predominantly pure lodgepole pine stands. The lodgepole pine cover type of the ABLA/VASC-PIAL phase and the ABLA/SPBE habitat type showed higher squirrel densities than expected by site favorability index. Higher levels were associated with moderate overstory diversity and relatively high basal areas of whitebark pine and Douglas-fir, respectively.



A



B

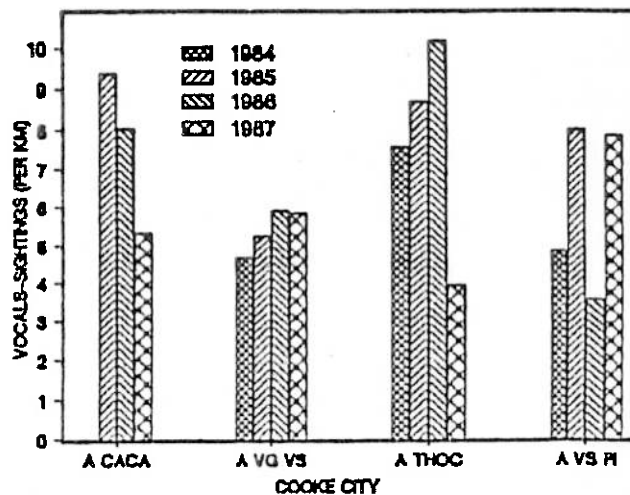
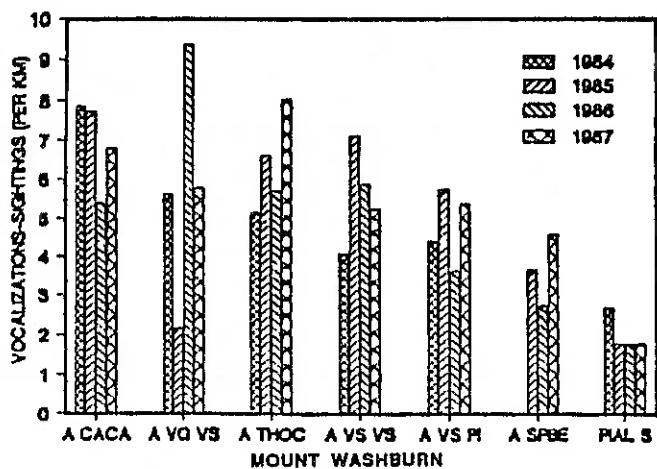


Figure 3—Linear densities of active squirrel middens and sightings + vocalizations for habitat types in the Mount Washburn (A) and Cooke City (B) study areas, 1984-1987.

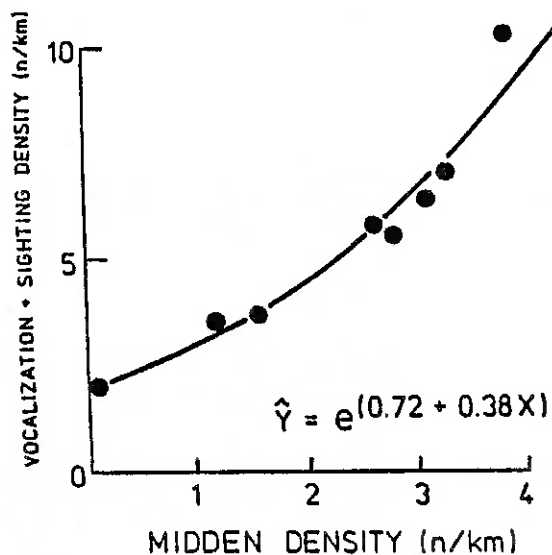


Figure 4—Relationship of average linear densities of squirrel middens and vocalizations + sightings for the Mount Washburn study area. Densities were averaged by habitat type and by habitat type and cover type for the ABLA/VASC-PIAL h.t.

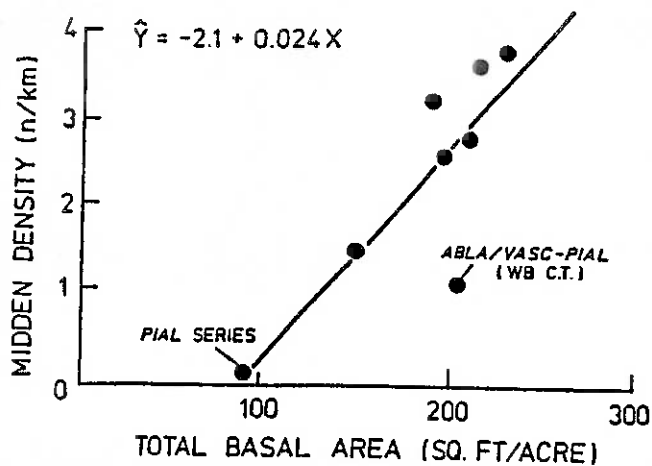


Figure 5—Relationship of active midden density and total timber basal area for the Mount Washburn study area.

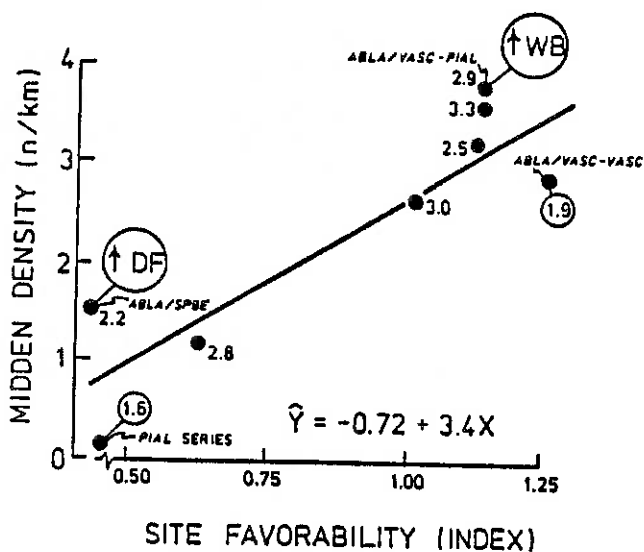


Figure 6—Relationship of active squirrel midden density and site favorability index for the Mount Washburn study area. Numbers at each datum are overstory diversity (H' ; Shannon and Weaver 1963) for the corresponding type.

DISCUSSION

Line transects have been used in previous studies to describe the relative abundance of wild populations (Burnham and others 1980; Eberhardt and others 1979; Hayne 1949). Indirect evaluation techniques have been useful measures of animal abundance when used to compare data between areas and time periods, or to associate habitat parameters with wildlife populations (Halvorson 1984). The following criteria should be met to reduce bias and variability in auditory and visual line transects of red squirrels (Eberhardt 1978; Halvorson 1984; Hayne 1949):

1. Sample design includes standardized methods that are repeatable.
2. Transects are laid out without bias toward the monitored population.
3. Time of day or season in relation to animal activity patterns does not vary over the course of the sampling period.
4. The effects of topography and cover on animal response to the observer are known.
5. Monitoring of a population is undertaken for a time period long enough to cover full cycles of population abundance.

This study of red squirrel populations appeared to have met these criteria. Red squirrel vocalizations could be heard between 0 to 60 m from transect lines, and usually occurred when the observer entered a red squirrel territory (C. Smith 1968). Red squirrels and middens were sighted between 0 to 40 m from the transect lines. There were no apparent differences in the frequency of squirrel calls or sightings related to time during daylight hours; stand boundaries and red squirrel territories were discrete so that topography changes were not critical to our evaluation. This study encompassed 4 years that included high, low, and intermediate whitebark pine cone crops. Although more years are needed to fully monitor red squirrel population trends (Halvorson 1984), some aspects of red squirrel habitat relationships can be addressed.

The high correlation of vocalization plus sighting densities with midden densities suggests that these two indices reflected the same phenomenon, and tends to corroborate the validity of each as a measure of squirrel abundance. The greater frequency of vocalization plus sighting densities relative to midden densities could have been a reflection of our greater sensitivity to red squirrel activity because of the greater detection range of vocalizations relative to middens. The exponential increase and greater variation of vocalizations and sightings with respect to middens could also reflect positive acoustical feedback similar to ruffed grouse (*Bonasa umbellus*) behavior (Rogers 1981). With increasing squirrel densities (midden densities), there could have been an exponential increase in vocalizations triggered as a positive response to one squirrel's initial call. We suspect that this second explanation holds, and so considered squirrel midden abundance to be a more reliable indicator of squirrel density in our study area.

The whitebark pine zone apparently constitutes an extreme of the red squirrel niche. Pure whitebark pine stands, represented by the PIAL series habitat types, were not hospitable habitats for red squirrels. Factors that may contribute to the lack of red squirrels in pure whitebark pine stands include less total overstory basal area and species diversity, highly variable cone crops characteristic of whitebark pine, and the high, cold, harsh environments associated with these stands. The more mesic and wetter habitat types supported more red squirrels. These habitats had more overstory diversity, which in turn offered red squirrels other species' cone crops when whitebark pine seeds were not available. Lodgepole

pine was an important conifer species to red squirrels. Although less preferred by red squirrels compared to some other tree species (Finley 1969), lodgepole pine played an important role in red squirrel habitat by providing a more consistent source of acrotinous and thus more storable cones (C. Smith 1968).

Annual variation in red squirrel densities apparently reflected general whitebark pine cone crops in stands with a moderate to high proportion of whitebark pine. This was most evident in the ABLA/VASC-PIAL phase of both the Cooke City and Mount Washburn study areas. Although cone crops of other conifer species in mixed stands were not measured in this study, they apparently played an important role in the red squirrels' food supply, especially in years of poor whitebark pine cone mast (Finley 1969). In general, squirrel densities in all habitat types were more sensitive to whitebark pine crops in the Mount Washburn study area where whitebark pine was more prevalent than in the Cooke City study area. Two factors may explain greater yearly fluctuations in red squirrel densities in stands with a substantial amount of whitebark pine:

1. The food supply associated with large whitebark pine cone crops may allow the temporary establishment of more territories and squirrels in areas that did not previously support red squirrels.
2. Bear depredation of red squirrel caches may compound the effects of variable whitebark pine crops by further disrupting the squirrel population social status, by competing for food, and by occasionally eating red squirrels outright. Squirrel remains show up in grizzly bear scats containing whitebark pine seeds (Knight and others 1987).

Regulatory factors have been identified for red squirrel populations in other study areas. C. Smith (1968) suggested that territoriality allowed individual red squirrels the optimum conditions for harvesting, storing, and defending a seasonal food supply throughout the year. He further demonstrated that territory size was related to food supply, or was inversely proportional to habitat quality. Kemp and Keith (1970) found a strong correlation between white spruce (*Picea glauca*) cone crops and red squirrel population levels. However, M. Smith (1968) showed that red squirrel populations could survive a white spruce cone crop failure by caching surplus cones during good mast years.

Red squirrel populations in our study areas may be influenced by bear use and flexible habitat requirements of squirrels. Our study area included the edge of occupied red squirrel habitat. In the whitebark pine zone this edge varied with whitebark pine cone production. In years of unusually large whitebark pine crops, red squirrels occupied pure whitebark pine stands (Kendall 1981). However, this occupancy was probably shortlived. We found little sign of permanent red squirrel occupancy in stands with a high percentage of whitebark pine. Generally, with increased site favorability and species diversity, middens were characterized by increasing amounts of cone debris that indicated a longer history of occupancy. Red squirrels apparently established transient territories

in whitebark stands during years of large cone crops because of the high forage quality of whitebark pine seeds. We are not sure how this was realized, but it was probably by the immigration of juveniles or extension of ranges by established squirrels into adjacent whitebark pine stands. Squirrels probably do not survive poor mast years in nearby pure whitebark pine stands because of frequent poor crops, the lack of alternative foods, and depredations by bears that possibly deprive them of an additional year's food. Ognev (1940) described a similarly dynamic situation for the European squirrel (*Sciurus vulgaris*) in the range of Asian stone pines (subsection *Cembrae*). He described transient territories and even mass "migrations" following years of crop failures.

More research is needed to better understand the relationships among whitebark pine, red squirrels, and bears, as well as how specific silvicultural treatments affect this system. Longer term study is required to assess red squirrel population responses to variable whitebark pine cone crops. In mixed and pure whitebark pine stands, red squirrel densities should be monitored, as should cone mast of all conifer species stratified by age and size classes. Study of red squirrel territory sizes with respect to different habitats or whitebark pine crops, as well as territory stability with respect to site favorability would provide valuable insight into red squirrel population regulation in this zone. More data are needed to assess the interaction between bears and red squirrel populations in the whitebark pine zone. This may be approached by relating levels of midden use by bears to annual variations in red squirrel densities and whitebark pine cone crops.

MANAGEMENT IMPLICATIONS

Timber management can potentially affect red squirrel population densities in the whitebark pine zone. Whitebark pine is not considered to be a valued commercial timber species (Arno and Hoff 1989). However, timber harvests do occur in stands that contain whitebark pine, primarily in stands of higher commercial value in the lower part of whitebark pine's elevational distribution. Basal area reduction by timber harvest in the whitebark pine zone will almost certainly reduce squirrel densities. Our results suggest this effect. Other studies in Alaska (Wolf and Zasada 1975) and Ohio (Nixon and others 1980) have also documented reduction in squirrel densities following reduction in basal area of seed-producing trees.

The strong link between red squirrels and grizzly bears (Kendall 1981; Mattson and Jonkel, this proceedings) in the whitebark pine zone merits the attention of resource managers. Management of grizzly bear habitat in the whitebark pine zone is partly contingent on management of red squirrel habitat and populations. Because of squirrel habitat requirements, management for both bears and squirrels logically revolves around maintenance of diverse species, high-basal-area stands on favorable, more mesic sites of the zone. Forest managers should be cautious when applying silvicultural practices in whitebark pine forests to "enhance" grizzly bear habitat. Leaving seed-bearing

whitebark pine trees in shelterwood cuts would reduce red squirrel densities by reducing overstory diversity and basal area. Planting whitebark pine seedlings following clearcutting may benefit long-term management of these stands, but will have little positive effect until these slow growing trees are mature enough to bear cones. Both practices would increase human access and activity. Increased risk of bear displacement and mortality would outweigh any gains achieved by overt forest manipulation.

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Mattson

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ron Lanner)—How many years is a squirrel midden likely to remain active?

A.—Middens of cone scales and cores in addition to cached cones are conspicuous signs of a red squirrel territory. They range in size from 1 to 300 m². Large middens can be decades old and represent the accumulation of many successive generations of red squirrels (Finley 1969). The advantage of a long-used, traditional site midden is that stored cone clippings help maintain cached cones in a moist, more storable condition.

Midden use is apparently short lived in predominant whitebark pine stands compared to other more diverse sites. Active middens can be recognized from inactive middens by the presence of fresh cones, cone clippings, and red squirrels at midden sites. In the predominant whitebark pine stands, we found active middens were generally smaller and newer than in other more mesic habitats. The proportion of all encountered middens found to be inactive was also higher in stands with a higher whitebark pine component. This may represent higher annual fluctuations in red squirrel abundance. This is consistent with our findings that pure whitebark pine stands are not favorable habitats for red squirrels.



United States
Department of
Agriculture

Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-217



Fig 9 - pg 22

Management Recommendations for the Northern Goshawk in the Southwestern United States

99 pg 22
Forest Service

Forage mixed S/F = 60% in SS6 (pg 28)

10,000 yf = 30

*GO NA
PFA mixed = 60+
S/F = 70+
Forage mixed = 60+ in OG
S/F nest BA = 140 (pg 14)*

Snags should be 18" log should be 12" 22-thin from below in nest area - fire on



*Forest health - 79
Saw all nests - 10
them nest - 22*

9/13

Geopieps - 60

Diversity = 32

*75-
19
Forage - 6
19
mil
mature
01c*

snaggo-17
ppage-83

Management Recommendations for the Northern Goshawk in the Southwestern United States

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VEGETATIVE STRUCTURAL STAGES:

Successional stages for a mixed-species forest ecosystem

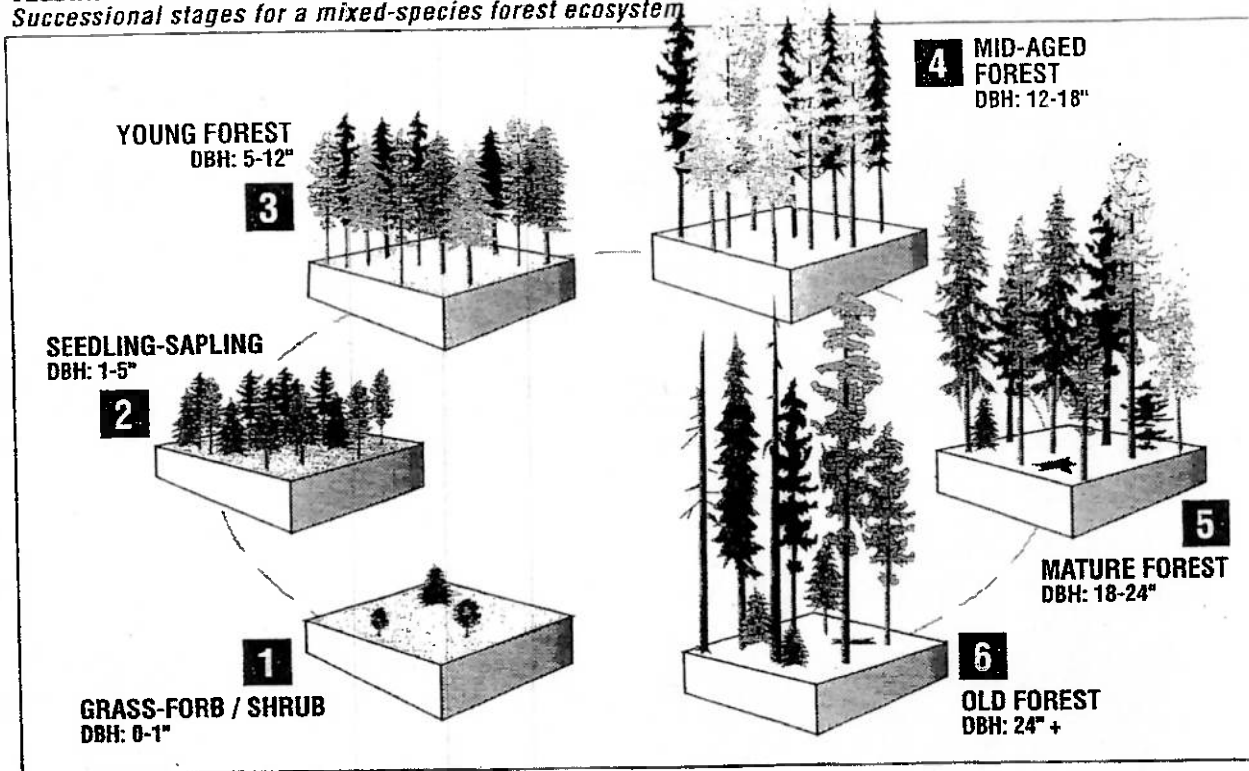


Figure 1. Forest vegetation structural stages and their associated diameter breast height (DBH) ranges.

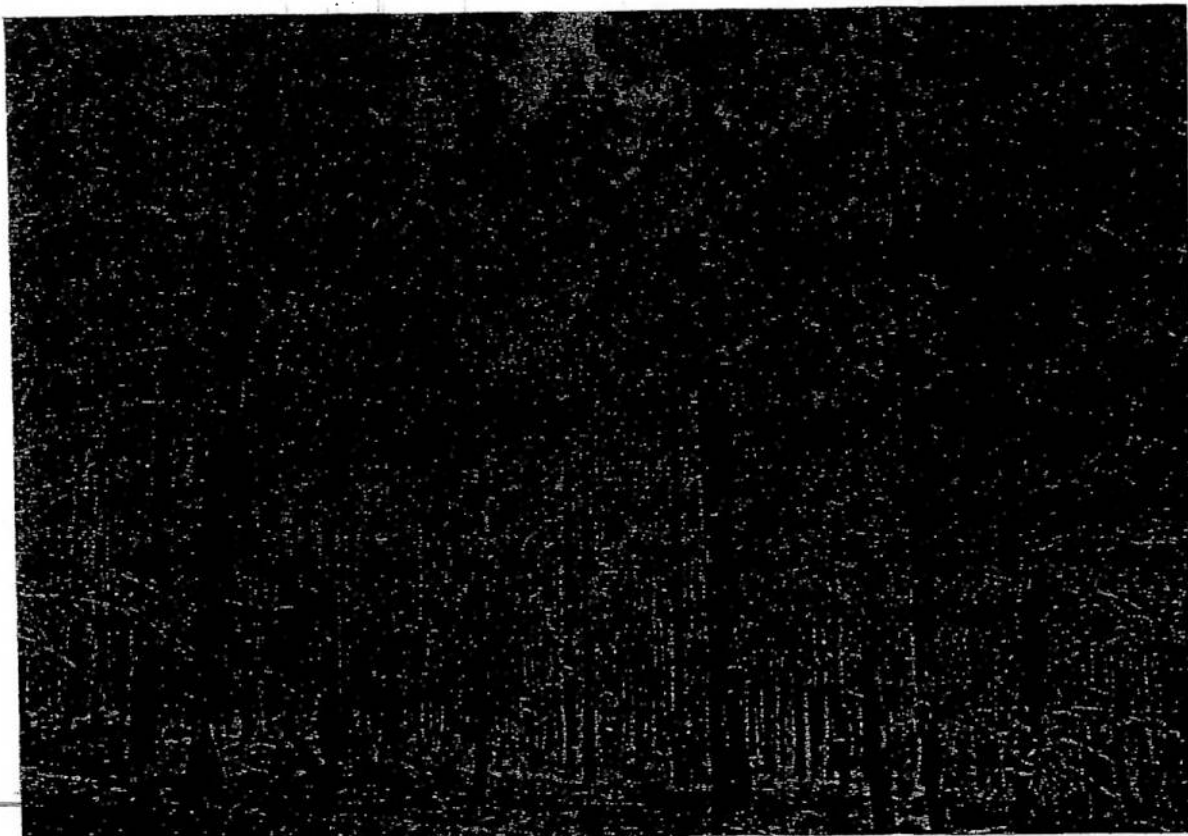


Figure 2. Dense "thicket" of small-diameter trees.

Table 1. Desired forest conditions in three forest types for sustaining northern goshawks and their principal prey species in the Southwest.

Attribute	Nest Area ^a	Home-Range Components			Foraging Area		
		Ponderosa Pine	Mixed-Species	Spruce-fir	Ponderosa Pine	Mixed-Species	Spruce-fir
VSS distribution ^b	0 ^c	10 ^c	10 ^c	10 ^c	10 ^c	10 ^c	10 ^c
grass/forb/shrub VSS 1 (%)	0	10	10	10	10	10	10
seedling-sapling VSS 2 (%)	0	20	20	20	20	20	20
young forest VSS 3 (%)	0	20	20	20	20	20	20
mid-aged forest VSS 4 (%)	100	20	20	20	20	20	20
mature forest VSS 5 (%)	100	20	20	20	20	20	20
old forest VSS 6 (%)	100	20	20	20	20	20	20
Canopy cover							
mid-aged forest VSS 4 ^c	NA ^d	1/3 60+ 2/3 50+	60+	60+	40+	1/3 60+ 2/3 40+	1/3 60+ 2/3 40+
mature forest VSS 5 (%)	50-70+	50+	60+	70+	40+	50+	60+
old forest VSS 6 (%)	50-70+	50+	60+	70+	40+	50+	60+
Years to mid-aged VSS 6	200-300	200-250	200-300	200-300	200-250	200-300	200-300
Opening size							
maximum size (acre)	NA	2	2	1	4	4	1
width--maximum (ft)	NA	200	150	125	200	200	125
Reserve trees ^e							
number of groups/acre	A ^f	1	1	2 ^h	1	1	2 ^h
number (per group)	NA	3-5	6	6	3-5	6	6
opening threshold ^g (acres)	NA	>1	>1	>0.5	>1	>1	>0.5
Snags (no/acre)	NR ⁱ	2	3	3	2	3	3
Downed logs (acre)	NR	3	5	5	3	5	5
Woody debris (tons/acre)	NR	5-7	10-15	10-15	5-7	10-15	10-15

^a Suitable nest areas only; attribute values may vary by forest type.^b VSS: Vegetation Structural Stages, a forest description based on the tree diameter distribution within a stand. For example, if the majority of the stems of a stand (based on basal area) were located in the 12-18 inch diameter class, the stand would be classified as a VSS 4. General diameter limits are: VSS 1= 0-1" DBH; VSS 2= 1-5" DBH; VSS 3= 5-12" DBH; VSS 4= 12-18" DBH; VSS 5= 18-24" DBH; VSS 6= 24"+ DBH.

DBH = Diameter at Breast Height (4.5 ft.).

^c Proportion of the area.^d NA; not applicable.^e Reserve trees; standing trees left after harvesting that will be allowed to become snags and downed logs.^f A; applicable, clumpiness, or groups of large trees is also desirable.^g When threshold size is exceeded, reserve trees are necessary.^h One group per 0.5 acres.ⁱ NR; not required, but presence of these features are not detrimental.

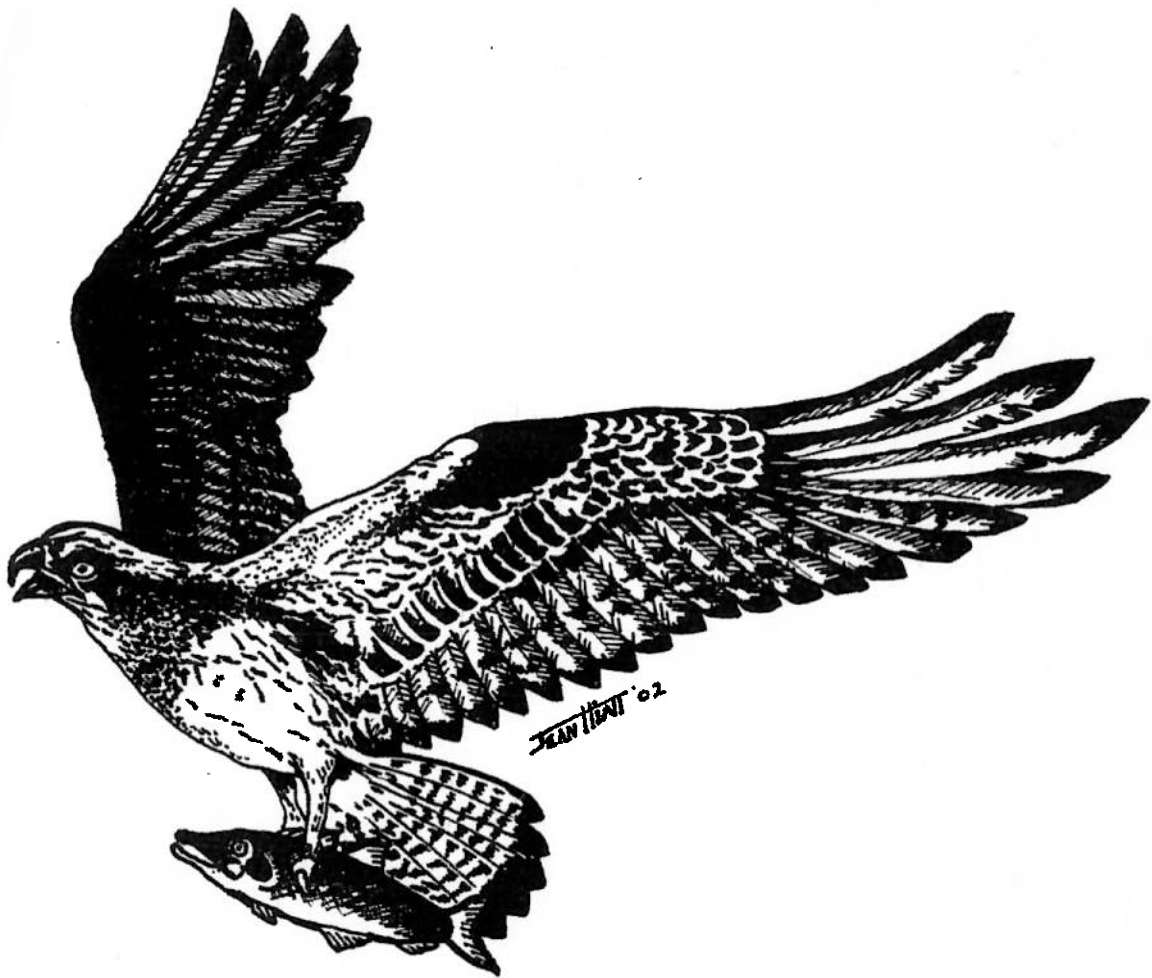
majority of
stem
basal
area

Table 2. Management recommendations for sustaining habitat for northern goshawks and its principal prey species in the Southwest.

Attribute	Home Range Components ^a		
	Nest Area	PFA	Foraging Area
Number of areas	6	1	1
Suitable ^a	3	NA	NA
Replacement ^a	3	NA	NA
Size (acre)	30 (Total =180)	420	5,400
Management season ^b	Oct-Feb	Oct-Feb	Year-long
Regeneration of forest			
Conifer	None	Yes	Yes
Aspen & Oak	None	Yes	Yes
Planting	None	Yes	Yes
Thinning from below ^a	Non-uniform spacing	Non-uniform spacing	Non-uniform spacing
Transportation system			
Road	Minimum density	Minimum density	Minimum density
Skid trails	Permanent	Permanent	Permanent
Forage utilization ^a (%)	20/40 ^c	20/40 ^c	20/40 ^c
Woody debris treatment	In Order of Preference		
Prescribed burning ^{a,d}	1	1	1
Lopping & Scattering ^a	2	2	2
Hand piling ^a	3	3	3
Machine grapple piling ^a	None	3	3
Dozer piling ^a	None	4	4

^a Refer to glossary of terms.^b For PFAs surrounding active nest areas, months in which management activities are allowed.^c Average forage utilization (percent by weight) in herbaceous layer/shrub layer; utilization should not exceed 40% of grasses and forbs and 60% of shrubs.^d Not applicable in spruce-fir forest type.

**UTAH FIELD OFFICE GUIDELINES FOR RAPTOR PROTECTION
FROM HUMAN AND LAND USE DISTURBANCES**



U.S. Fish and Wildlife Service, Utah Field Office
Salt Lake City
January 2002 update

Prepared by Laura A. Romin and James A. Muck

Table 2. Nesting periods and recommended buffers for raptors in Utah

Species	Spatial Buffer (miles)	Seasonal Buffer	Incubation, # Days	Brooding, # Days Post-Hatch	Fledging, # Days Post-Hatch	Post-fledge Dependency to Nest, # Days ¹
Bald eagle	1.0	1/1-8/31	34-36	21-28	70-80	14-20
Golden eagle	0.5	1/1-8/31	43-45	30-40	66-75	14-20
N. Goshawk	0.5	3/1-8/15	36-38	20-22	34-41	20-22
N. Harrier	0.5	4/1-8/15	32-38	21-28	42	7
Cooper's hawk	0.5	3/15-8/31	32-36	14	27-34	10
Ferruginous hawk	0.5	3/1-8/1	32-33	21	38-48	7-10
Red-tailed hawk	0.5	3/15-8/15	30-35	35	45-46	14-18
Sharp-shinned hawk	0.5	3/15-8/31	32-35	15	24-27	12-16
Swainson's hawk	0.5	3/1-8/31	33-36	20	36-40	14
Turkey vulture	0.5	5/1-8/15	38-41	14	63-88	10-12
California condor	1.0	NN yet	56-58	5-8 weeks	5-6 months	2 months
Peregrine falcon	1.0	2/1-8/31	33-35	14-21	35-49	21
Prairie falcon	0.25	4/1-8/31	29-33	28	35-42	7-14
Merlin	0.5	4/1-8/31	28-32	7	30-35	7-19
American kestrel	NN ²	4/1-8/15	26-32	8-10	27-30	12
Osprey	0.5	4/1-8/31	37-38	30-35	48-59	45-50
Boreal owl	0.25	2/1-7/31	25-32	20-24	28-36	12-14
Burrowing owl	0.25	3/1-8/31	27-30	20-22	40-45	21-28
Flammulated owl	0.25	4/1-9/30	21-22	12	22-25	7-14
Great horned owl	0.25	12/1-9/31	30-35	21-28	40-50	7-14
Long-eared owl	0.25	2/1-8/15	26-28	20-26	30-40	7-14
N. saw-whet owl	0.25	3/1-8/31	26-28	20-22	27-34	7-14
Short-eared owl	0.25	3/1-8/1	24-29	12-18	24-27	7-14
Mex. Spotted owl	0.5	3/1-8/31	28-32	14-21	34-36	10-12
N. Pygmy owl	0.25	4/1-8/1	27-31	10-14	28-30	7-14
W. Screech owl	0.25	3/1-8/15	21-30	10-14	30-32	7-14
Common Barn-owl	NN ²	2/1-9/15	30-34	20-22	56-62	7-14

¹ Length of post-fledge dependency period to parents is longer than reported in this table. Reported dependency periods reflect the amount of time the young are still dependent on the nest site; i.e. they return to the nest for feeding.

² Due to apparent high population densities and ability to adapt to human activity, a spatial buffer is not currently considered necessary for maintenance of American kestrel or Common barn-owl populations. Actions resulting in direct mortality of individual birds or take of known nest sites is unlawful.

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SUMMARY

Proponents of land-use activities are responsible for determining potential impacts to raptors of those activities. Appropriate management strategies for conservation and restoration of raptor populations and their habitats associated with the proposed actions should be devised. The following steps should become routine during initial project planning:

1. Coordinate with appropriate U.S. Fish and Wildlife Service (Service), Utah Division of Wildlife Resources (UDWR), and/or land management agency wildlife biologists at the onset of project planning.
2. Identify species and distribution of raptors occurring within the project area by evaluating existing data and/or conducting on-site surveys.
3. Determine location and distribution of important raptor habitat, raptor nests, and available prey base associated with proposed developments and activities.
4. Ascertain the type, extent, timing, and duration of development or human activities proposed to occur.
5. Consider cumulative effects to raptors of proposed projects when added to past, present, and reasonably foreseeable actions.
6. Minimize, to the extent feasible, loss of raptor habitats and avoid long-term habitat degradation. Mitigate for unavoidable losses of high-valued raptor habitats, including (but not limited to) nesting, winter roosting, and foraging areas.
7. Plan and schedule short-term and long-term project disturbances and human-related activities to avoid raptor nesting and roosting areas, particularly during crucial breeding and wintering periods.
8. Post-project and post-mitigation monitoring are necessary to document stability of raptor populations and their prey base, and to evaluate success of mitigation efforts.

PREFACE

The following raptor protection guidelines were prepared by the Service in coordination with various federal, state, tribal, and private entities with an interest in raptor protection. These guidelines are intended to provide an advisory framework for consistent raptor management approaches statewide.

Table 3. Recommended proportion (None, Half, or Full) of the species-specific spatial buffer zones for level and duration of activities during raptor nesting				
NESTING PHENOLOGY (Risk Level)				
	Courtship and Nesting (High)	Incubation, and Brooding (High)	Post-Brooding Nestling Period (Moderate)	Post Fledging Dependency (Moderate)
In-Vehicle, Recreational^a Activity: Any recreational vehicle driving off-road, or on dirt roads, and not part of a routinely used transportation corridor.				
less than 1 hour ^b	NONE	NONE	NONE	NONE
less than 1 hour ^c	HALF	HALF	NONE	NONE
greater than 1 hour	FULL	FULL	HALF	HALF
Out-of-Vehicle, Recreational Activity: including, but not limited to hiking, dispersed camping, rock climbing, birdwatching, fishing, hunting, biological surveys.				
less than 1 hour ^b	HALF	HALF	NONE	NONE
less than 1 hour ^c	FULL	FULL	HALF	HALF
greater than 1 hour	FULL	FULL	FULL	FULL
Developed Recreation: including, but not limited to ski resorts, snowmobile and off-road vehicle courses, developed campground sites, and group tour operations.				
	FULL	FULL	FULL	FULL
Industrial, Municipal, and Transportation Disturbance: including, but not limited to urbanization; mining; oil and gas development; logging; power line construction; road construction & maintenance; use of explosives; agricultural operations; fixed wing and helicopter overflights.				
less than 1 hour ^b	FULL	FULL	HALF	HALF
less than 1 hour ^c	FULL	FULL	FULL	HALF
greater than 1 hour	FULL	FULL	FULL	FULL

^a Recreational activities are defined as those providing outdoor recreation, entertainment, or adventure.

^b No more than 1 repetition in a 24 hour period for a duration of less than 1 hour is allowable.

^c More than one repetition per 24 hours, spaced no less than 2 hours apart, occurs during daylight hours. Full buffer zone is required for any activities occurring during nighttime hours

to minimize disturbance to raptors and raptor nest sites.

STEP 3

Apply the information attained in Steps 1 and 2 to the following guidelines for occupied and unoccupied nest sites to avoid or minimize effects of proposed land use activities to nesting raptors:

- **Occupied raptor nests:** Activities should not occur within the spatial/seasonal buffer of any nest (occupied or unoccupied) when raptors are in the process of courtship and nest site selection. Egg laying, incubation, fledging, brooding, and post-fledging dependency periods are protected by varying seasonal and spatial buffers (Tables 2 and 3).

Short term land use and human use activities should only proceed within the spatial buffer of an occupied nest outside the seasonal buffer, after coordination with appropriate Service, UDWR, and/or land management agency biologists. Mitigation for habitat loss or degradation should be planned. Long term land use activities and human use activities should not occur within the species-specific spatial buffer zone of occupied nests.

- **Unoccupied raptor nests:** If a nest site within a territory is deemed unoccupied after sufficient time has elapsed in a specified breeding season and prior to the beginning of the next year's breeding season, human activity could be allowed within the nesting area. This period varies dependent on raptor species. However, as a general rule, even renesting will usually not occur later than May 30 (C. White, BYU, 1998, pers. comm.).

Short term land use and human activities may progress near a nest or nest territory designated as unoccupied. For long term land use activities, unoccupied nests should be protected for 7 years, or the period a known preferred prey species fluctuates from population highs to lows. At the end of the 7-year period, each nest should be evaluated by a qualified wildlife biologist as to its potential future use. Criteria could include the raptor species current population trend in the local area, the corresponding prey species population levels and trends, as well as past, current, and future impacts of the proposed action. Nests could also be considered permanently abandoned if the nest has been physically damaged past the point of repair by raptors.

Long-term land use activities and human use activities should not occur proximally to unoccupied nests unless it is determined that mitigation is appropriate and can be accomplished prior to initiation of the long-term disturbance. Coordination with Service, UDWR, and/or land management agency

Monitoring and documentation of results is recommended following any of the aforementioned techniques to maximize success of efforts. Publishing data and results should also be considered to widely circulate information regarding success of raptor mitigation techniques.

CONCLUSION

It has been the intent of these guidelines to provide land use planners with the tools to develop successful raptor management and mitigation strategies proximal to disturbances from land use activities. Raptor survey information-attained-through implementation of these guidelines will also provide a means to track raptor population trends and document population responses to human use of their environments.

The guidelines have presented recommendations for protection of raptor life stages (i.e., nesting and wintering) as well as raptor habitats. The recommendations are hardly exhaustive of available protective strategies, nor are all recommendations intended to be incorporated on every proposed project. Coordination with appropriate Service, UDWR, and/or land management agency biologists is important during the analysis of project impacts and selection of protective measures.

Project proponents should seek first to avoid or minimize impacts. Where there are inevitable losses or degradations of habitat or disturbance to individual birds, mitigation can be incorporated to lessen the impact. Overall, these guidelines have been designed to maintain viable raptor populations amid continued human use of the environment.

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Decline of the North American avifauna

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Species extinctions have defined the global biodiversity crisis, but extinction begins with loss in abundance of individuals that can result in compositional and functional changes of ecosystems. Using multiple and independent monitoring networks, we report population losses across much of the North American avifauna over 48 years, including once common species and from most biomes. Integration of range-wide population trajectories and size estimates indicates a net loss approaching 3 billion birds, or 29% of 1970 abundance. A continent-wide weather radar network also reveals a similarly steep decline in biomass passage of migrating birds over a recent 10-year period. This loss of bird abundance signals an urgent need to address threats to avert future avifaunal collapse and associated loss of ecosystem integrity, function and services.

Slowing the loss of biodiversity is one of the defining environmental challenges of the 21st century (1–5). Habitat loss, climate change, unregulated harvest, and other forms of human-caused mortality (6, 7) have contributed to a thousand-fold increase in global extinctions in the Anthropocene compared to the presumed prehuman background rate, with profound effects on ecosystem functioning and services (8). The overwhelming focus on species extinctions, however, has underestimated the extent and consequences of biotic change, by ignoring the loss of abundance within still-common species and in aggregate across large species assemblages (2, 9). Declines in abundance can degrade ecosystem integrity, reducing vital ecological, evolutionary, economic, and social services that organisms provide to their environment (8, 10–15). Given the current pace of global environmental change, quantifying change in species abundances is essential to assess ecosystem impacts. Evaluating the magnitude of declines requires effective long-term monitoring of population sizes and trends, data which are rarely available for most taxa.

Birds are excellent indicators of environmental health and ecosystem integrity (16, 17), and our ability to monitor many species over vast spatial scales far exceeds that of any other animal group. We evaluated population change for 529 species of birds in the continental United States and Canada (76% of breeding species), drawing from multiple standardized bird-monitoring datasets, some of which provide close to fifty years of population data. We integrated range-wide estimates of population size and 48-year population trajectories,

along with their associated uncertainty, to quantify net change in numbers of birds across the avifauna over recent decades (18). We also used a network 143 weather radars (NEXRAD) across the contiguous U.S. to estimate long-term changes in nocturnal migratory passage of avian biomass through the airspace in spring from 2007 to 2017. The continuous operation and broad coverage of NEXRAD provide an automated and standardised monitoring tool with unrivaled temporal and spatial extent (19). Radar measures cumulative passage across all nocturnally migrating species, many of which breed in areas north of the contiguous U.S. that are poorly monitored by avian surveys. Radar thus expands the area and the proportion of the migratory avifauna that is sampled relative to ground surveys.

Results from long-term surveys, accounting for both increasing and declining species, reveal a net loss in total abundance of 2.9 billion (95% CI = 2.7–3.1 billion) birds across almost all biomes, a reduction of 29% (95% CI = 27–30%) since 1970 (Fig. 1 and Table 1). Analysis of NEXRAD data indicate a similarly steep decline in nocturnal passage of migratory biomass, a reduction of 13.6 ± 9.1% since 2007 (Fig. 2A). Reduction in biomass passage occurred across the eastern U.S. (Fig. 2, C and D), where migration is dominated by large numbers of temperate- and boreal-breeding songbirds; we observed no consistent trend in the Central or Pacific flyway regions (Fig. 2, B to D, and table S5). Two completely different and independent monitoring techniques thus signal major population loss across the continental avifauna.

Species exhibiting declines (57%, 303/529) based on long-

term survey data span diverse ecological and taxonomic groups. Across breeding biomes, grassland birds showed the largest magnitude of total population loss since 1970—more than 700 million breeding individuals across 31 species—and the largest proportional loss (53%); 74% of grassland species are declining (Fig. 1 and Table 1). All forest biomes experienced large avian loss, with a cumulative reduction of more than 1 billion birds. Wetland birds represent the only biome to show an overall net gain in numbers (13%), led by a 56% increase in waterfowl populations (Fig. 3 and Table 1). Surprisingly, we also found a large net loss (63%) across 10 introduced species (Fig. 3, D and E, and Table 1).

A total of 419 native migratory species experienced a net loss of 2.5 billion individuals, whereas 100 native resident species showed a small net increase (26 million). Species overwintering in temperate regions experienced the largest net reduction in abundance (1.4 billion), but proportional loss was greatest among species overwintering in coastal regions (42%), southwestern aridlands (42%), and South America (40%) (Table 1 and fig. S1). Shorebirds, most of which migrate long distances to winter along coasts throughout the hemisphere, are experiencing consistent, steep population loss (37%).

More than 90% of the total cumulative loss can be attributed to 12 bird families (Fig. 3A), including sparrows, warblers, blackbirds, and finches. Of 67 bird families surveyed, 38 showed a net loss in total abundance, whereas 29 showed gains (Fig. 3B), indicating recent changes in avifaunal composition (table S2). While not optimized for species-level analysis, our model indicates 19 widespread and abundant landbirds (including 2 introduced species) each experienced population reductions of >50 million birds (data S1). Abundant species also contribute strongly to the migratory passage detected by radar (19), and radar-derived trends provide a fully independent estimate of widespread declines of migratory birds.

Our study documents a long-developing but overlooked biodiversity crisis in North America—the cumulative loss of nearly 3 billion birds across the avifauna. Population loss is not restricted to rare and threatened species, but includes many widespread and common species that may be disproportionately influential components of food webs and ecosystem function. Furthermore, losses among habitat generalists and even introduced species indicate that declining species are not replaced by species that fare well in human-altered landscapes. Increases among waterfowl and a few other groups (e.g., raptors recovering after the banning of DDT) are insufficient to offset large losses among abundant species (Fig. 3). Importantly, our population loss estimates are conservative since we estimated loss only in breeding populations. The total loss and impact on communities and ecosystems could be even higher outside the breeding season

if we consider the amplifying effect of “missing” reproductive output from these lost breeders.

Extinction of the Passenger Pigeon (*Ectopistes migratorius*), once likely the most numerous bird on the planet, provides a poignant reminder that even abundant species can go extinct rapidly. Systematic monitoring and attention paid to population declines could have alerted society to its pending extinction (20). Today, monitoring data suggest that avian declines will likely continue without targeted conservation action, triggering additional endangered species listings at tremendous financial and social cost. Moreover, because birds provide numerous benefits to ecosystems (e.g., seed dispersal, pollination, pest control) and economies (47 million people spend 9.3 billion U.S. dollars per year through bird-related activities in the U.S. (21)), their population reductions and possible extinctions will have severe direct and indirect consequences (10, 22). Population declines can be reversed, as evidenced by the remarkable recovery of waterfowl populations under adaptive harvest management (23) and the associated allocation of billions of dollars devoted to wetland protection and restoration, providing a model for proactive conservation in other widespread native habitats such as grasslands.

Steep declines in North American birds parallel patterns of avian declines emerging globally (14, 15, 22, 24). In particular, depletion of native grassland bird populations in North America, driven by habitat loss and more toxic pesticide use in both breeding and wintering areas (25), mirrors loss of farmland birds throughout Europe and elsewhere (15). Even declines among introduced species match similar declines within these same species' native ranges (26). Agricultural intensification and urbanization have been similarly linked to declines in insect diversity and biomass (27), with cascading impacts on birds and other consumers (24, 28, 29). Given that birds are one of the best monitored animal groups, birds may also represent the tip of the iceberg, indicating similar or greater losses in other taxonomic groups (28, 30).

Pervasiveness of avian loss across biomes and bird families suggests multiple and interacting threats. Isolating spatio-temporal limiting factors for individual species and populations will require additional study, however, since migratory species with complex life histories are in contact with many threats throughout their annual cycles. A focus on breeding season biology hampers our ability to understand how seasonal interactions drive population change (31), although recent continent-wide analyses affirm the importance of events during the non-breeding season (19, 32). Targeted research to identify limiting factors must be coupled with effective policies and societal change that emphasize reducing threats to breeding and non-breeding habitats and minimizing avoidable anthropogenic mortality year-round. Endangered species legislation and international treaties, such as

Table 1. Net change in abundance across the North American avifauna, 1970-2017. Species are grouped into native and introduced species, management groups (landbirds, shorebirds, waterbirds, waterfowl), major breeding biomes, and nonbreeding biomes (see data S1 in (18) for assignments and definitions of groups and biomes). Net change in abundance is expressed in millions of breeding individuals, with upper and lower 95% credible intervals (CI) shown. Percentage of species in each group with negative trend trajectories are also noted. Values in bold indicate declines and loss; those in italics indicate gains.

Species Group	Number of Species	Net Abundance Change (Millions) & 95% CI			Percent Change & 95% CIs			Proportion Species in Decline
		Change	LC95	UC95	Change	LC95	UC95	
Species Summary								
All N. Am. Species	529	-2,911.9	-3,097.5	-2,732.9	-28.8%	-30.2%	-27.3%	57.3%
All Native Species	519	-2,521.0	-2,698.5	-2,347.6	-26.5%	-28.0%	-24.9%	57.4%
Introduced Species	10	-391.6	-442.3	-336.6	-62.9%	-66.5%	-56.4%	50.0%
Native Migratory Species	419	-2,547.7	-2,723.7	-2,374.5	-28.3%	-29.8%	-26.7%	58.2%
Native Resident Species	100	26.3	7.3	46.9	5.3%	1.4%	9.6%	54.0%
Landbirds	357	-2,516.5	-2,692.2	-2,346.0	-27.1%	-28.6%	-25.5%	58.8%
Shorebirds	44	-17.1	-21.8	-12.6	-37.4%	-45.0%	-28.8%	68.2%
Waterbirds	77	-22.5	-37.8	-6.3	-21.5%	-33.1%	-6.2%	51.9%
Waterfowl	41	34.8	24.5	48.3	56.0%	37.9%	79.4%	43.9%
Aerial Insectivores	26	-156.8	-183.8	-127.0	-31.8%	-36.4%	-26.1%	73.1%
Breeding Biome								
Grassland	31	-717.5	-763.9	-673.3	-53.3%	-55.1%	-51.5%	74.2%
Boreal forest	34	-500.7	-627.1	-381.0	-33.1%	-38.9%	-26.9%	50.0%
Forest Generalist	40	-482.2	-552.5	-413.4	-18.1%	-20.4%	-15.8%	40.0%
Habitat Generalist	38	-417.3	-462.1	-371.3	-23.1%	-25.4%	-20.7%	60.5%
Eastern Forest	63	-166.7	-185.8	-147.7	-17.4%	-19.2%	-15.6%	63.5%
Western forest	67	-139.7	-163.8	-116.1	-29.5%	-32.8%	-26.0%	64.2%
Arctic Tundra	51	-79.9	-131.2	-0.7	-23.4%	-37.5%	-0.2%	56.5%
Aridlands	62	-35.6	-49.7	-17.0	-17.0%	-23.0%	-8.1%	56.5%
Coasts	38	-6.1	-18.9	8.5	-15.0%	-39.4%	21.9%	50.0%
Wetlands	95	20.6	8.3	35.3	13.0%	5.1%	23.0%	47.4%
Nonbreeding Biome								
Temperate North America	192	-1,413.0	-1,521.5	-1,292.3	-27.4%	-29.3%	-25.3%	55.2%
South America	41	-537.4	-651.1	-432.6	-40.1%	-45.2%	-34.6%	75.6%
Southwestern Aridlands	50	-238.1	-261.2	-215.6	-41.9%	-44.5%	-39.2%	74.0%
Mexico-Central America	76	-155.3	-187.8	-122.0	-15.5%	-18.3%	-12.6%	52.6%
Widespread Neotropical	22	-126.0	-171.2	-86.1	-26.8%	-33.4%	-19.3%	45.5%
Widespread	60	-31.6	-63.1	1.6	-3.7%	-7.4%	0.2%	43.3%
Marine	26	-16.3	-29.7	-1.2	-30.8%	-49.1%	-2.5%	61.5%
Coastal	44	-11.0	-14.9	-6.7	-42.0%	-51.8%	-26.7%	68.2%
Caribbean	8	-6.0	1.4	-15.7	12.1%	-2.8%	31.7%	25.0%

Clark's nutcracker breeding season space use and foraging behavior

TD Schaming

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Considering the entire life history of a species is fundamental to developing effective conservation strategies. Decreasing populations of five-needle white pines may be leading to the decline of Clark's nutcrackers (*Nucifraga columbiana*). These birds are important seed dispersers for at least ten conifer species in the western U.S., including whitebark pine (*Pinus albicaulis*), an obligate mutualist of Clark's nutcrackers. For effective conservation of both Clark's nutcrackers and whitebark pine, it is essential to ensure stability of Clark's nutcracker populations. My objectives were to examine Clark's nutcracker breeding season home range size, territoriality, habitat selection, and foraging behavior in the southern Greater Yellowstone Ecosystem, a region where whitebark pine is declining. I radio-tracked Clark's nutcrackers in 2011, a population-wide nonbreeding year following a low whitebark pine cone crop, and 2012, a breeding year following a high cone crop. Results suggest Douglas-fir (*Pseudotsuga menziesii*) communities are important habitat for Clark's nutcrackers because they selected it for home ranges. In contrast, they did not select whitebark pine habitat. However, Clark's nutcrackers did adjust their use of whitebark pine habitat between years, suggesting that, in some springs, whitebark pine habitat may be used more than previously expected. Newly extracted Douglas-fir seeds were an important food source both years. On the other hand, cached seeds made up a relatively lower proportion of the diet in 2011, suggesting cached seeds are not a reliable spring food source. Land managers focus on restoring whitebark pine habitat with the assumption that Clark's nutcrackers will be available to continue seed dispersal. In the Greater Yellowstone Ecosystem, Clark's nutcracker populations may be more likely to be retained year-round when whitebark pine restoration efforts are located adjacent to Douglas-fir habitat. By extrapolation, whitebark pine restoration efforts in other regions may consider prioritizing restoration of whitebark pine stands near alternative seed sources.

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WOODPECKER PREDATION ON BARK BEETLES IN ENGELMANN SPRUCE LOGS AS RELATED TO STAND DENSITY

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Abstract

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Eighty Engelmann spruce logs (*Picea engelmannii* Parry), which were distributed in open (bulldozed to clearcut), semi-open (selectively cut), and dense (uncut) spruce forest, were infested with *Dendroctonus obesus* (Mann.) and *Ips pilifrons* Sw. and fed upon by northern three-toed and hairy woodpeckers. Sections of the infested boles were covered with screen to prevent woodpecker feeding and all logs were left in the field over one winter and through the following summer. By spring, the spruce beetle brood was reduced approximately 50% in all three forest areas. By fall, the spruce beetle brood suffered a 71, 83 and 52% reduction in the open, semi-open and dense forest, respectively. Spruce beetles appeared to be in greatest numbers in the semi-open forest, resulting in the greatest woodpecker predation there. Woodpeckers did not feed in the open meadows. Estimates in the spring, before the *Ips* emerged from the logs, showed that woodpeckers reduced the *Ips* brood by 76 and 11% in the open and semi-open forest, respectively. *Ips* were not found in dense forest or in meadows.

Introduction

The spruce beetle, *Dendroctonus obesus* (Mann.), is an important economic pest. Epidemic numbers of this beetle killed 4.3 billion board feet of timber in western Colorado during 1939-1951 (Massey and Wygant 1954). Past studies in Colorado (Baldwin 1960, 1968a, b; Hutchison 1951; Knight 1958; Koplin 1967; Massey and Wygant 1954; Yeager 1955; and others) have shown that woodpeckers are an important natural predator of the spruce beetle and can inflict up to 98% mortality on the developing brood in standing trees (Knight 1958). In wind-thrown trees, northern three-toed and hairy woodpeckers (*Picoides tridactylus* (Linn.) and *Dendrocopos villosus* (Linn.)) have reduced the spruce beetle brood by 70-79% (Baldwin 1968a). The per cent mortality of spruce beetle broods attributed to woodpecker predation is dependent upon both the position (standing or horizontal) of the infested tree (Knight 1958; Baldwin 1968a) and the intensity of the spruce beetle infestation (Koplin 1967). Koplin found that woodpeckers ate 28, 84 and 53% of the total beetle population in endemic, epidemic and large epidemic situations, respectively.

Ips pilifrons Sw., a secondary bark beetle of little economic importance, is usually found with spruce beetles. *Ips* are thought to play a minor role in the predator-prey relationship between woodpecker and spruce beetle; however, little is known about woodpecker predation on them.

In Colorado, local infestations of spruce and *Ips* beetles occur in over-mature standing trees, windthrown trees, or in debris and cull logs from logging operations. The latter are considered to be an important potential source of epidemic outbreaks of bark beetles. One factor contributing to the success of woodpecker predation on bark beetle broods might be the density of forest in which debris

¹Research was conducted while Mr. Shook was employed by the Rocky Mountain Forest and Range Experiment Station, U.S. Dept. Agric., Forest Serv., Fort Collins, Colo.

Ips / Debris Adapted

*- 6 fold increase
woods in infested
vs uninfested
stands.*

*- Ips in
cull logs -
debris
- secondary bark
beetle*

*Wind throw:
45% in logged
38% in unlogged*

*Logged: 40 snag/ha
unlogged: 70*

even logs!

and cull logs occur. It would be useful to the forester to know in what tree densities woodpecker predation on spruce and *Ips* beetles is maximized.

The purpose of this study was to determine the magnitudes of predation on spruce and *Ips* beetle broods by woodpeckers on horizontal logs in graded densities of Engelmann spruce (*Picea engelmannii* Parry) forest.

Methods

A 3-sq.-mile study area was established at an endemic infestation of spruce beetles at Beaver, Amethyst, and Saint Charles creeks in the Wet Mountains of the San Isabel National Forest, 5 miles northwest of San Isabel City, Custer County, Colo. Portions of this area had previously been logged (in 1959 and 1963), and the logged area contained windthrown trees, logging debris, and cull logs. Intermingled within the study area were four distinguishable stand types: open, semi-open, dense, and meadows. The open areas ranged from land cleared by tractors of most of the standing trees to such densities of standing culls and snags as are accepted within the clearcut category in local forestry practice. The semi-open areas had been selectively logged, while the dense areas were uncut, closed forest. The meadows were large areas free of trees. The highest spruce beetle population in the study area was estimated to be 6880 emerging adults per acre in 1965; however, woodpeckers and other mortality factors had reduced this population to endemic size, 400-1000 beetles per acre, by 1967 (Baldwin 1968a).

In June 1967, 80 Engelmann spruce trees with a diameter at breast height of approximately 10 in. were felled in the forest stands. Twelve sets of six logs each were distributed throughout the study area. Each set consisted of two logs in each of the open, semi-open, and dense areas. Separate from these, four sets of two logs each were distributed in the meadows. Since trees were not found in the meadows or in some open areas, the trees that were to be placed in these areas were felled along the nearest forest edge. All trees were left in situ until mid-July to absorb attacks from *Ips* and spruce beetles. During the third week of July, the trees that had been cut along the forest edge were dragged to their respective meadow or open area. When the density of beetles in these trees was later compared to that in other trees that were cut in place, no significant difference was found, except in the case of the logs dragged to the meadows. In these, the density of spruce beetles was comparable to that in other logs, but surviving *Ips* were not found.

The lack of space between bark and ground has been reported as a limiting factor to woodpecker predation (Baldwin 1968a); therefore, the infested logs were held off the ground either by branches or short logs propped under one end to provide access to woodpeckers. The distance from the ground averaged 1.2 ft.

In August 1967, a cage of 0.5 in. mesh hardware cloth 3 ft in width was placed around the bole of each log and held away from the bark with wooden blocks 1.25 in. thick. These cages were placed toward the basal part of the infested stems where there were fewer branches protruding. The cages were always placed where woodpeckers would not be restricted from the bark surface on either side of the cage. The cage prevented woodpeckers from feeding on the caged portion of the log, and it is assumed the presence of the cage did not affect the bark beetles.

The logs were sampled for the density of surviving spruce beetles and *Ips* in June and August 1968. Sampling was carried out by removing a 6-in.-wide band of bark from both the caged and uncaged portions of each log and counting the living beetles in and under the bark. The length of egg galleries in each sample

6880/ac!
less access
by woodpeckers!



Growth, Chemistry, and Genetic Profiles of Whitebark Pine Forests Affected by Climate-Driven Mountain Pine Beetle Outbreaks

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Climate change-driven *Dendroctonus ponderosae* outbreaks in semi-naïve *Pinus albicaulis* may result in rapid natural selection for trees with genotypes and phenotypes associated with survival. In this study, we investigated whether survivors were genetically and chemically different from a living cohort of trees that escaped predation due to smaller size and estimated genetic diversity. We also examined how growth rate and climate sensitivity varied between beetle-killed and surviving trees. *Dendroctonus ponderosae* predominantly kills large diameter trees; therefore, we predicted that large surviving trees would have distinctive genetic profiles and, due to bottlenecks and drift, survivors would have lower genetic diversity than the abundant smaller mature trees that escaped predation. We found survivors were indeed genetically divergent from the smaller trees but, contrary to expectations, the smaller trees had lower diversity. This suggests that while beetles may select for trees with particular genotypes, other factors are also driving population genetic sub-structuring. Individual tree terpene profiles were diverse and varied by population but showed no clear relationship to survivorship. Two groups of trees with divergent sensitivities to climate were observed in each population, but neither was a clear indicator of survivorship or susceptibility to beetle attack. Growth rate was the best predictor of survivorship with survivors growing significantly slower than beetle-killed trees over their lifetimes although growth rates converged in years just prior to increased beetle activity. Overall, our results suggest that *P. albicaulis* forests show considerable divergence among populations and within-population genetic sub-structuring, and that they may contain complex mosaics of adaptive potentials to a variety of stressors including *D. ponderosae*. To protect the ability of this tree to adapt to increasing pressure from beetles, blister rust, and climate change, a top priority should be the maintenance of standing genetic diversity and adaptive shifts in allele frequencies.

Keywords: *Dendroctonus ponderosae* (mountain pine beetle), genetic diversity, climate change, adaptation, dendrochronology, *Pinus albicaulis*

INTRODUCTION

A recent outbreak of *Dendroctonus ponderosae* (mountain pine beetle) in *Pinus albicaulis* (whitebark pine) has killed trees across large areas. *Pinus albicaulis* is a semi-naïve host for *D. ponderosae* (Raffa et al., 2013). It grows in the subalpine zone where cold typically protects it from predation by the beetle. Exceptions occur when warm droughts allow beetles to move upslope and kill trees until normal colder conditions return (Perkins and Swetnam, 1996). However, chronic warming due to climate change has allowed the beetle to persist in many subalpine areas of western North America supporting outbreaks and widespread mortality of mature *P. albicaulis* (Buotte et al., 2016, 2017; Six et al., 2018). Outbreaks are expected to select for increased resistance in tree hosts over time and selection pressure may be especially strong in a naïve non-coevolved host that lacks a co-evolutionary history with the beetle. In such forests, most trees can be expected to have low levels of defense resulting in high levels of mortality of susceptible genotypes leaving behind rare individuals that exhibit some degree of resistance.

As has been observed in other naïve hosts experiencing outbreaks of *D. ponderosae* (Clark et al., 2010; Cudmore et al., 2010; Raffa et al., 2013; Burke et al., 2017), *P. albicaulis* appears to have more reduced defenses than populations of *Pinus* that have experienced regular pressure from the beetle (Raffa et al., 2017). This has led to fears that the tree may experience severe declines or even local extinction in areas where the beetle is now resident. However, survival of some mature *P. albicaulis* in forests hard-hit in recent *D. ponderosae* outbreaks, and the discovery that these trees may be genetically distinct from those that are chosen for attack, indicates adaptation may be occurring in response to increased selection pressure by the beetle (Six et al., 2018). Little research has investigated the possibility of rapid *in situ* adaptation in conifers due to climate change-driven insect outbreaks. Most bioclimatic models assume that all individuals of a tree species respond similarly and typically incorporate only a few broad ecological parameters (Rice and Emery, 2003; Aitken et al., 2008). These models seldom include phenotypic plasticity, genetic diversity, local adaptation, or the potential for near-term evolution, factors that could lead to substantially different outcomes (Davis and Shaw, 2001; Harte et al., 2004; Savolainen et al., 2007; Aitken et al., 2008). Clearly, there is a need for genetic and phenotypic data to inform our understanding of the potential for evolution to support *in situ* persistence of tree species to improve model outcomes and to inform conservation approaches.

The ability of *P. albicaulis* to adapt (here defined as an increase in allele frequencies associated with favorable changes in phenotypes) to increased bark beetle pressure, white pine blister rust (a disease caused by an invasive pathogen, *Cronartium ribicola*), and changes in climate, will rely to a great degree, on the genetic diversity already existing within affected populations or accessible through gene flow (Kremer et al., 2012, 2014). Many forest trees, including conifers, have high levels of genetic diversity that result in a variety of tree responses to environmental conditions both within and among populations (Savolainen et al., 2007; Kremer et al., 2012; McDowell et al., 2020). This variability

forms the basis for subsequent evolution at local scales and may support considerable *in situ* adaptation in response to climate change (Petit and Hampe, 2006). For *P. albicaulis* to persist in the face of increasing pressure by *D. ponderosae* and changing environmental conditions, shifts not only in allele frequencies supporting resistant phenotypes, but also the maintenance of standing genetic diversity, will be crucial.

Conifers are often viewed as slow to evolve because they are long-lived and wind-pollinated. However, many have shown a considerable capacity for rapid local adaptation even with extensive gene flow (Petit and Hampe, 2006). In fact, populations of trees that experience high mortality rates via highly selective agents such as insects and drought may be the fastest to evolve in response to new climatic conditions (Kuparinen et al., 2010). Climate change can lead to increased rates of adaptation of trees both directly and indirectly. Direct effects include decreased or enhanced growth or increased mortality rates in response to changes in temperature and precipitation (Kremer et al., 2014). These, in turn, can initiate a cascade of indirect effects including altered levels of biotic disturbance. This can currently be seen globally where warming temperatures are leading to greater survival and reproductive rates of many forest insects, and tree hosts stressed by drought or heat are becoming more vulnerable to insect herbivory (Jactel et al., 2019; Kolb et al., 2019).

Aggressive tree-killing bark beetle population dynamics are intimately linked to climatic conditions affecting insect demographics and tree physical and chemical defenses (Raffa et al., 2016). Warming can lead to higher beetle population growth rates (Creeden et al., 2014) and highly selective host tree choice by bark beetles can result in differential mortality among trees of the same species due to selection for specific size classes and a suite of other traits, independent of stress (Stephenson et al., 2019). Aggressive bark beetles choose individual trees for colonization using a combination of visual and chemical cues that results in either the initiation of a pheromone-mediated mass attack or rejection (Raffa et al., 2016). The type and quantity of secondary defense chemicals produced by a tree, especially terpenoids, help beetles locate trees, both at a distance, and upon contact (Raffa and Smalley, 1995; Keeling and Bohlmann, 2006; Tittiger and Blomquist, 2017). Additionally, bark beetles exploit several monoterpenes to produce the aggregation pheromones they use to initiate and sustain the mass attacks that allow them to overcome tree defenses (Seybold et al., 2000). The production of secondary defensive chemicals is strongly influenced by tree genotype (Keeling and Bohlmann, 2006; Bullington et al., 2018), which leads to variation in the chemical profiles expressed by individual trees, influencing their relative attractiveness to beetles. Furthermore, trees experiencing drought stress can exhibit decreases in constitutive and induced defenses (Arango-Velez et al., 2011) suggesting that shifts in tree chemistry in response to water deficit may influence the ability of beetles to successfully attack trees. However, how this may translate to effects on beetle choice of individual trees is unclear. In piñon pine, Trowbridge et al. (2019) found that increased emission rates of terpenoids during warm periods were offset by decreases in production resulting in no net change in emission rates overall. This may generally be the case, but more work is

produce different types, amounts, or ratios of secondary chemical compounds that result in the rejection of these trees by beetles but that the chemicals involved are in groups other than the terpenoids we included.

It is not known whether larger resin duct area results in greater constitutive defense. If it does then there should be greater resin flow in slow growing *P. albicaulis*. However, resin flow in *P. albicaulis* is usually very low and sometimes non-existent. During this study, we measured resin flow over a 24-h period in July 2017 for 40 survivors and 40 generals at Vipond Park and only four trees produced measurable, but low, amounts of resin with two falling into each category (data not shown). Additionally, larger resin ducts in other conifers have not been found to result in greater resin flow (Hodges et al., 1981; Hood and Sala, 2015). Slow-growing survivors may invest more in producing greater resin duct area and resin within their xylem, but the effect on beetles may be more qualitative than quantitative, especially if they also invest differently in the secondary chemicals they produce. An investigation into the secondary chemistry of *P. albicaulis* with differing resin duct areas may help identify the means by which beetles can exert 'choice at a distance' given survivors are not attacked and beetles do not encounter resin physically.

Interestingly, climate sensitivity was not predictive of tree survivorship. At Poverty Flat and Vipond Park, beetle-killed trees and survivors both contained large proportions of sensitive and non-sensitive trees (Supplementary Appendices 2, 3). Our results agree with those of Cooper et al. (2018) who found no relationship of climate variables to survivorship in *P. contorta* and of Kichas et al. (2020) who found no relationship of these variables to survivorship or resin duct area in *P. albicaulis*.

In correlations comparing BAI/BAs for individual trees and climate variables, again we found no clear difference in climate sensitivity between survivors, beetle-killed trees, and generals (Table 8). However, we did find differences between sensitive and non-sensitive trees, particularly a positive correlation to PDSI indicating a negative growth response of sensitive trees to drier conditions (Supplementary Appendices 2–4). In contrast, non-sensitive trees did not respond positively to PDSI, but rather, were more likely to positively respond to March temperatures or negatively to December temperatures (CO). Warmer March temperatures may allow for earlier growth in these trees while the negative relationship to December temperature may relate to negative effects of warmer temperatures on snowpack retention. Kichas et al. (2020) observed reduced growth during wetter winters for *P. albicaulis* at a site in northern Montana and Perkins and Swetnam (1996) noted positive responses to winter and spring precipitation on growth of *P. albicaulis* and suggested that feedbacks among climate variables likely produce nonlinear effects influencing snowpack and consequently growth (Perkins and Swetnam, 1996). The sensitive-insensitive dichotomy that we observed in tree responses to climate variables at all three sites further suggests that genetic sub-structuring within *P. albicaulis* populations increases the diversity of tree responses to climatic conditions, potentially increasing resilience of the forest as a whole to fluctuating conditions over time.

There appeared to be a relationship of drought to outbreak development at Poverty Flat and Vipond Park (Supplementary Figures 2, 3) but no relationship at Lacy Creek (Supplementary Figure 3). In fact, Lacy Creek trees did not reduce growth rates during the most recent drought and actually exhibited dips in growth during wet periods in the 60s and 90s. This highlights the importance of tree responses, and likely genetics, along with climate in outbreak development.

Importance to Conservation

Whitebark pine is in decline across much of its range due to the effects of the non-native disease white pine blister rust, *D. ponderosae* outbreaks, and climate change (Keane et al., 2012). This is a 'wicked problem' in that successful conservation of this tree will require approaches that deal with all three threats. However, as different as these threats are from one another, they share one commonality, and that is that the ability of the species to persist will depend on its potential for adaption to these stressors that, in turn, depends on genetic diversity.

Standing genetic diversity is in large part how long-lived organisms such as trees persist in the face of shifting climatic and other stressors over time (Petit and Hampe, 2006). We found evidence of substantial population sub-structuring in *P. albicaulis* that may indicate a strong adaptive potential. Different cohorts and categories of trees within each population exhibited divergent genetic (Figure 1) and phenotypic profiles (Figures 2, 3) as well as differential responses to climate (Table 8). Older trees possessed greater genetic diversity (Table 2) but younger (general) trees grew better under more recent conditions (Figure 4) suggesting they may be better adapted to warmer conditions. Although generals had lower genetic diversity, gene flow among other cohorts including large survivors should act to maintain genetic diversity and to produce new genetic combinations on which selection can act. However, the rapid growth rates exhibited by generals may also be a cause for concern given that *D. ponderosae* appears to prefer faster growing trees. This may influence overall stand survival and genetic diversity as these trees reach sizes susceptible to beetle attack. Overall, our results suggest *P. albicaulis* forests contain a complex mosaic of adaptive potentials to a variety of stressors but that the ability of populations to persist will likely vary across the geographic range of the tree depending in the genetic diversity within and among populations (Jorgenson and Hamrick, 1997; Liu et al., 2016).

To protect the ability of this tree to adapt to current and future conditions, the maintenance of genetic diversity should be a top priority, and practices that can reduce diversity or that may introduce maladaptive genes or swamp local adaptation should be avoided. Reliance on natural regeneration is best because it involves locally adapted seed sources drawn from the full array of diversity present in the stand and seedlings that establish will have done so under a local climatic selection filter. Where silvicultural practices are applied, they should be implemented with caution. In cases where planting is required, care should be used in sourcing seed, as even locations close to one another may not be appropriate for collections. For example, trees at Lacy Creek and Vipond Park, located only 27 km apart, showed differences in genetic and terpenoid profiles, growth rates, and sensitivity to

climate. Even when using seed from the site where seedlings will be planted, care must be taken to collect from multiple cohorts, as one cohort may not reflect the full genetic diversity of the site as shown by differences between survivors and generals at our sites. To maximize effectiveness and minimize inadvertent harm, it will be crucial in all conservation efforts to consider the strength of local adaptation and genetic structuring within and among populations as well as the sources and degree of gene flow and the multitude of stressors with which the tree must contend (McKay et al., 2005).

Our results also indicate that thinning prescriptions aimed at increasing tree growth in whitebark pine should be applied with considerable caution. Greater tree ring width/faster growth has been widely used as a proxy for tree vigor and as an indicator of greater resistance to bark beetles (Bhuyan et al., 2017). This view has led to thinning projects in whitebark pine aimed at increasing growth and vigor (Retzlaff et al., 2018) and resistance to *D. ponderosae*. However, while the relationship between growth and resistance to beetles has been shown to be positive in some pines and variable in others (Millar et al., 2012; Knapp et al., 2013; Keen et al., 2020), the opposite appears to be true for some populations of *P. contorta* (Cooper et al., 2018) and for *P. albicaulis*. In our study, as well as in that of Kichas et al. (2020), faster overall growth was the strongest predictor of mortality due to *D. ponderosae* indicating that such treatments will not have their intended effect in *P. albicaulis* and may even be detrimental. Furthermore, naturally low resin production, even by survivor and open-grown *P. albicaulis*, indicates thinning will have little-to-no effect on enhancing constitutive defenses against the insect.

Anthropogenic change is creating or enhancing a number of stressors on forests. To aid forests in adapting to these stressors, we need to move beyond traditional spacing and age-class prescriptions and take into account the genetic variability within and among populations and the impact our actions may have on adaptive potential and forest trajectories. Because so little is known about the genetic diversity in most forest trees, and because it is key to effective conservation, studies of genetic diversity and structuring in forest trees should be a top priority in forest adaptation and conservation efforts.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

DS conceived of the study, participated in all aspects of collections and analysis, and wrote the manuscript. DP did most sample collections in Idaho and participated in project conception and writing. EB did much of the sample processing for genetic and tree ring analysis, and oversaw data management. DS conducted genetic analyses and along with PB conducted the statistical analyses of tree growth and climate with help from JH. GB conducted the chemical analyses while DS, AT, and MH conducted the statistical analysis and interpretations of the data. All the authors contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fgc.2021.671510/full#supplementary-material>

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The Influence of Mammals and Birds in Retarding Artificial and Natural Reseeding of Coniferous Forests in the United States

Clarence F. Smith and Shaler E. Aldous¹

FORESTERS have long been searching for an economical method of re-establishing trees on deforested lands. Three methods have been used, namely: the planting of nursery-raised stock and natural seedlings, direct seeding, and the encouragement of natural reproduction. To date the planting program has been given the most attention but the other two methods are older and considerable hope for their satisfactory use is always being expressed. Chief among the factors that have pushed reproduction by seeding into the background is the depredation of seed-eating rodents and birds.

This does not mean, however, that animals are the chief factors in preventing reforestation. Among the many other important factors are: availability of seed source, soil type and condition, prevalence of destructive insects and diseases, moisture supply, temperature, slope, and many others. So it should not be inferred that if rodent and bird pressures could be removed reforestation would always be successful. The role of mammals and birds in aiding reforestation is not discussed in this paper. Although actual consumption of coniferous seeds implies destruction, it must be recalled that in the process of feeding, mammals through caching, and birds by transportation and dropping of seeds may function as seed distributors.

The first known effort at direct seeding on a national forest in the United States was in 1901 (11) on the San Bernardino National Forest, California. This and several other trials (12, 38) failed due to a combination of factors, one of which was the activity of seed-eating animals. Periodic attempts at direct seeding were continued with little or no success through about 1912 (6, 20, 27, 39, 59, 62). In the early twenties an interest was again shown in this work (30, 41, 42, 50), but still one of the main obstacles to success was the animal factor. During the late thirties and up until the present time, a renewed interest has again been extended to this

method of reforestation (1, 2, 8, 10, 16, 25, 26, 32, 33, 34, 35, 36, 37, 40, 45, 46, 47, 48, 49, 58, 61, 63).

It has been during this latter period that the authors and other workers in the Fish and Wildlife Service have been making extensive investigations of the relation of animals to the forest. Reproduction by seed and the animal pressure thereon has received considerable attention. It is the purpose of this paper to point out the degree and type of pressure exerted by birds and mammals on forest seeds, the tree species affected, and to describe methods of reducing or eliminating these losses.

MANY ANIMAL AND BIRD SEED EATERS

A large number of different mammals and birds feed on the seeds of coniferous trees, both when supplied naturally and when provided by planting procedures. From the literature and the authors' studies, a total of 44 mammals and 37 birds have been found to eat coniferous seeds (Table 1). This list could be materially lengthened if the data from unpublished stomach analyses in the files of the Fish and Wildlife Service were assembled. Van Dersal (64) lists the animals that feed on all species of conifers in the United States, but from his descriptions it is impossible to separate seed eaters from vegetative feeders.

Although the list of seed eaters is long, only a few species are of significance in forest regeneration. The tree squirrels, chipmunks, white-footed mice, and a few species of seed-eating fringillid birds are responsible for the greater part of all trouble caused by mammals and birds in regenerating forests by seeding. Habitat is the governing factor which determines which species of animal might be present to consume the seeds.

Tree squirrels (*Sciurus*) are not commonly found very far from trees with the result that their depredations are usually on the cones or on the seed dropping from them. On denuded areas that are being artificially reseeded, these squirrels are of minor importance except around the tree-fringed borders. On the other hand, they

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TABLE 1.—LIST OF BIRDS AND MAMMALS KNOWN TO EAT THE SEEDS OF CONIFEROUS TREES
(AND THE AUTHORITY REFERENCE)¹

Common name	Scientific name	Reference
Birds		
✓Blue grouse	<i>Dendragapus obscurus</i>	4
Sierra grouse	<i>Dendragapus fuliginosus sierrae</i>	52
Ruffed grouse	<i>Bonasa umbellus</i>	52
Bobwhite	<i>Colinus virginianus</i>	8
California quail	<i>Lophortyx californicus</i>	52
Band-tailed pigeon	<i>Columba fasciata</i>	52
Eastern mourning dove	<i>Zenaidura macroura carolinensis</i>	8, 58, 60
✓Red-shafted flicker	<i>Colaptes cafer collaris</i>	57
✓Lewis woodpecker	<i>Asyndesmus lewis</i>	52
Canada jay	<i>Perisoreus canadensis</i>	59
Blue jay	<i>Cyanocitta cristata</i>	59
✓Steller's jay	<i>Cyanocitta stelleri</i>	52, 57
✓Crow	<i>Corvus brachyrhynchos</i>	52
✓Clark's nutcracker	<i>Nucifraga columbiana</i>	52
✓Winter wren	<i>Nannus hiemalis</i>	36
✓Robin	<i>Turdus migratorius</i>	15, 59
English sparrow	<i>Passer domesticus</i>	59
Southern meadowlark	<i>Sturnella magna argutula</i>	8
Red-wing blackbird	<i>Agelaius phoeniceus</i>	8
Rusty blackbird	<i>Euphagus carolinus</i>	8
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	8
Blackbirds	No species named	15, 59
Cowbird	<i>Molothrus ater</i>	8
Bronzed grackle	<i>Quiscalus quisculus aeneus</i>	15
Blue grosbeak	<i>Guitra caerulea</i>	59
✓Evening grosbeak	<i>Hesperiphona vespertina</i>	52
✓California purple finch	<i>Carpodacus purpureus californicus</i>	36
✓Pine grosbeak	<i>Pinicola enucleator</i>	52
✓Redpoll	<i>Acanthis linaria</i>	59
✓Goldfinch	<i>Spinus tristis</i>	Text
✓Red crossbill	<i>Loxia curvirostra</i>	52
Towhee	<i>Pipilo maculatus</i>	36
✓Slate-colored junco	<i>Junco hyemalis hyemalis</i>	Text
Carolina junco	<i>Junco hyemalis connectens</i>	13
Oregon junco	<i>Junco oregonus</i>	36
Red-backed junco	<i>Junco phaeonotus dorsalis</i>	39, 52
✓Chipping sparrow	<i>Spizella passerina</i>	2
Song sparrow	<i>Melospiza melodia</i>	36
Mammals		
Cinereous shrew	<i>Sorex cinereus</i>	Text
Trowbridge shrew	<i>Sorex Trowbridgii</i>	37
Wandering shrew	<i>Sorex vagrans</i>	37
Baird's dusky shrew	<i>Sorex obscurus bairdi</i>	37
Yaquina shrew	<i>Sorex yaquinae</i>	37
Gibbs shrew-mole	<i>Neurotrichus gibbsii</i>	37
Columbia ground squirrel	<i>Citellus beecheyi</i>	23
Rock squirrel	<i>Citellus variegatus</i>	24
California ground squirrel	<i>Citellus beecheyi</i>	23
Fisher ground squirrel	<i>Citellus beecheyi fisheri</i>	52
White-tailed antelope squirrel	<i>Citellus leucurus</i>	24
Mantled ground squirrel	<i>Citellus lateralis</i>	24, 59
	<i>Citellus lateralis arizonensis</i>	57
	<i>Citellus lateralis chrysodeirus</i>	52
✓Western chipmunk	<i>Eutamias minimus</i>	52
	<i>Eutamias minimus jacksoni</i>	Text
	<i>Eutamias amoenus</i>	52
	<i>Eutamias quadrivittatus</i>	52
	<i>Eutamias quadrivittatus speciosus</i>	52
	<i>Eutamias cinereicollis</i>	52, 57
	<i>Eutamias townsendii</i>	26, 52
	<i>Eutamias quadrimaculatus</i>	52
	<i>Eutamias sp.</i>	12, 30, 49, 58, 61
✓Eastern chipmunk	<i>Tamias striatus striatus</i>	53
	<i>Tamias striatus griseus</i>	Text

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are probably the heaviest consumers of coniferous seeds under natural conditions. Heavy cutting of sugar pine cones (even before they are mature) by the California gray squirrel was reported by Berry (6) and Jotter (27). As much as 70 to 75 percent of the seed crop was reported taken by these squirrels and as many as 702 ponderosa pine cones were found under one tree.

VORACIOUS RODENTS ARE HEAVY SEED CONSUMERS

The appetite for pine seeds by squirrels was shown by Hatt (18) when he reported one pair of captive red squirrels ate the seeds from 422 cones of eastern white pine in one week's time. Mollenhauer (35) found red squirrels clipped from 50 to 100 percent of the cone-bearing limbs of the table mountain pine. It was the opinion of Pulling (41) that red squirrels took all the white pine seed produced during a poor year in one area in New York State. An examination of three red squirrel stomachs from a jack pine slash area in Minnesota showed that they had consumed 1,178 jack pine seeds or an average of 392 seeds per squirrel. In this latter case, the squirrels were collected at the edge of the cutting area. None was observed in the main body of the clearing. This localization was further illustrated by Smith (53) when he wrote, "The greatest rodent damage occurred on the fully-timbered area where red squirrels invaded

the quadrats several times searching for ungerminated seeds."

Ground squirrels (*Citellus*) are not commonly pests on sites requiring reforestation. These animals occur only in the western states in open types of habitat where reforestation is not likely to be practiced. However, these animals are known to retard forest regeneration at times, as Tinsley (58) reported the Columbian ground squirrel in Idaho to have consumed practically all the seeds (ponderosa and western white pine) sown.

One associated quite closely with the forest is the mantled squirrel. Throughout the ponderosa pine belt, this group is common and believed to be an important ponderosa pine seed consumer by Wahlenberg (60) and Taylor and Gorsuch (57).

Chipmunks play an important role in preventing the reseeding of forests. The western chipmunk (*Eutamias*) has been a greater factor in this respect than the eastern form (*Tamias*). Most seeding studies have been made in the West and in the Lake States where the western form is much more abundant. In the Lake States, both chipmunks occupy the same range, but *Eutamias* is found more in the logged or burned areas and is much more numerous over the whole area.

In northern Minnesota, chipmunks were found to be pronounced pine seed destroyers. The examination of stomachs from 88 chipmunks col-

TABLE 1.—(Continued)

Common name	Scientific name	Reference
Red squirrel	<i>Tamiasciurus hudsonicus</i>	5, 9, 15, 26, 29, 41, 43, 49, 53, 56
	<i>Tamiasciurus hudsonicus baileyi</i>	41, 43, 49, 53, 56, 18
	<i>Tamiasciurus hudsonicus loquax</i>	65
	<i>Tamiasciurus hudsonicus ventorum</i>	21
	<i>Tamiasciurus hudsonicus richardsoni</i>	36, 54
	<i>Tamiasciurus douglasii</i>	36, 52
	<i>Tamiasciurus douglasii albolimbatus</i>	17
	<i>Tamiasciurus fremonti fremonti</i>	19
Western gray squirrel	<i>Sciurus griseus</i>	36, 52
Flying squirrel	<i>Glaucomys sabrinus latipes</i>	3
Pocket mouse	<i>Perognathus fasciatus</i>	Text
	<i>Perognathus parvus mollipilosus</i>	51
Kangaroo rat	<i>Dipodomys heermanni</i>	52
White-footed mouse	<i>Peromyscus maniculatus</i>	52
	<i>Peromyscus maniculatus gracilis</i>	Text
	<i>Peromyscus leucopus noveboracensis</i>	53
	<i>Peromyscus sp.</i>	55, 62
Woodrat	<i>Neotoma fuscipes</i>	14
Red-backed mouse	<i>Clethrionomys gapperi</i>	Text
Meadow mouse	<i>Microtus montanus</i>	58
House mouse	<i>Mus musculus</i>	53

This list does not include species eating Juniper and Taxis, and includes references only from published articles and findings from the author's field work.

lected in a jack pine slash area revealed that 72 percent contained the remains of jack pine seeds. They averaged 31 seeds per stomach, but one chipmunk had eaten 796 and another had 204 in its stomach and 168 in its cheek pouches. The 88 animals had disposed of a total of 2,749 jack pine seeds. Although chipmunks formed only 39.5 percent of the rodent population, they consumed 61 percent of the jack pine seeds removed by rodents on this area.

Coniferous seed destruction by chipmunks has been reported by Dearborn (12) from the Black Hills, Tinsley (58) in the Northern Rocky Mountains, Korstian and Baker (30) in the intermountain region of Utah, Taylor and Gorsuch (57) in the Southwest, Willis (62) and Moore (36) in the Pacific Northwest, L. Smith (53) for the New England area, and Horn, in an unpublished (1932) report from California.

Mice as a group, because of their wide habitat and geographic distribution, are perhaps the greatest animal factor in retarding forest regeneration by seeds. A great many of the authors reviewed, mentioned mice as one of the chief offenders.

White-footed mice (*Peromyscus*) have been found by the authors to be the most widely distributed and the most influential species in their studies. Where other authors have specified species, the white-footed group are usually mentioned. According to Silver (50), white-footed mice damaged from 10 to 90 percent of the seed spots on a planting program in the Ocala National Forest, Florida, Willis (62) attributed 98 percent failure of seed spots of Douglas-fir on the Columbia National Forest to the work of mice, and cage tests showed that a mouse could consume 300 seeds of this species daily. In the Lake States white-footed mice were found to be second only to chipmunks in numbers and in the consumption of jack pine seeds. The examination of 30 stomachs revealed that 70 percent had eaten jack pine seeds and the whole lot averaged 19 seeds per stomach. The greatest number eaten by a single animal was 156.

Other mice known to feed on coniferous seeds are red-backed mice (*Clethrionomys*), meadow mice (*Microtus*), jumping mice (*Zapus*), pocket mice (*Perognathus*), and house mice (*Mus musculus*).

The red-backed mice are perhaps the most characteristic forest species, but their food preferences run more to succulent vegetation than to

seeds. After a logging operation where most of the timber is cut, these mice are rapidly replaced by the white-footed species. That they can be a minor factor in seed consumption, however, is shown by the analysis of 59 stomachs of mice trapped on a jack pine slash area. Only 14 percent of them had eaten jack pine seed, the greatest number per individual being 25, and the average .6.

BIRDS ALSO TAKE MUCH SEED

Birds are more of an influence in seed consumption than is generally believed. Many workers have referred to seed destruction by birds and rodents but few have specified which birds are involved. As early as 1916, Toumey (59) listed mourning doves, redpoll, Canada jay, blue jay, English sparrow, robin, blackbird, finch, junco, and blue grosbeak as forest seed eaters. In the longleaf pine area of Mississippi, Burleigh (8) found heavy consumption of seeds by mourning doves, bobwhites, meadow larks, Brewer's rusty, and red-winged blackbirds, and cowbirds. He found that damage by these birds was most severe during years of heavy seed production and relatively light during scanty seed years, the explanation being that the seed crop when abundant attracted and held larger bird populations. Pearson (39) and Krauch in a 1937 report for the southwest named the junco as a cause of failure of seeding experiments.

In the northwest, Moore (36) found Douglas-fir seeds attractive to winter wrens, purple finches, song sparrows, towhees, and juncos.

Four juncos, eight chipping sparrows, eight goldfinches, and one Brewer's blackbird were collected on a jack pine slash area in northern Minnesota. Of these 21 birds only three (chipping sparrows) had failed to feed on jack pine seeds. Most of these birds were present in fair-sized flocks, which could have been responsible for the consumption of a large part of the seed crop.

It is rather surprising to find such insectivorous mammals as shrews consuming coniferous seeds, but Moore (37) states, "They play a definite and deleterious part in natural reforestation." He lists five species of shrews that were found to eat Douglas-fir seeds. Jack pine seeds were found in the stomach of one long-tailed shrew in Minnesota.

Many workers have deplored serious losses of seed by rodents and birds without specifying the identity of the animals concerned. In fact, the writers have found it impossible to attribute

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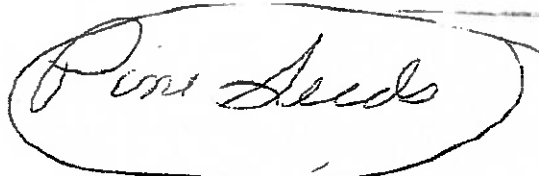
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Competition Among Insects, Birds and Mammals for Conifer Seeds

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Synopsis Species of at least 5 orders of insects, 6 families of birds, and 2 orders of mammals, in various combinations, can exploit the cones and seeds of most species of conifers. Lodgepole pine is the exception to this pattern of broad taxonomic diversity of seed predators in that only pine squirrels and coreid bugs attack its serotinous cones. The contrast between lodgepole pine and other conifers demonstrates that large intrinsic variation in the abundance of a resource fosters the evolution of a broad range of taxonomic groups to exploit the resource. The diverse groups are limited by different predators and alternate resources when conifer seeds independently decrease in abundance.

INTRODUCTION

Because conifers are such an important source of lumber, a great amount of effort has been put into the study of their biology (Fowells, 1965), their seeds (USDA, 1974), and the predators of their seeds (Keen, 1958). People concerned with the lumber industry are interested in how many seeds escape predation to allow reforestation of logged or burned areas. Questions of general biological interest that do not relate directly to reforestation may go unasked even though pertinent information is available. In this paper, we use the extensive literature on conifer seeds and their predators to outline the nature of these seeds as a food resource and the manner in which the various seed predators use this resource. The information can then be used as a basis for answering three questions: 1) Why are there many different distantly related taxa of animals exploiting a distinctive and easily delimited resource? 2) How do the various taxa interact in using the resource? 3) How do the different taxa avoid competitive ex-

clusion? Our personal experience is mainly limited to the conifers of western North America and our discussion will be concentrated on those, although some of the patterns probably apply generally to conifers in the Northern Hemisphere (Bock and Lepthien, 1976).

THE RESOURCE

As a food resource, single viable conifer seeds are highly uniform as to size (weight of female gametophyte and embryo) and quality (caloric value of female gametophyte and embryo) within an individual cone, tree or species population (Table 1). The total number of viable seeds in single cones within a single annual crop for one tree or a species population is more variable than seed size or quality, especially in lodgepole pine (*Pinus contorta* Dougl.) (Table 1). The sizes of annual cone crops for single trees or species populations are by far the most variable feature of conifer seeds in all western North American species, except lodgepole pine (Table 1).

The variation in caloric value of seeds given in Table 1 is probably an underestimation because 5 to 10 seed kernels were burned to derive each value thus masking the variation between individual seeds. The similar variations between samples from the same cone, cones from the same tree,

We wish to thank Jim Reichman for stimulating us to think about competition between distantly related taxa. Gary Bateman and Gilbert Schubert made helpful comments in reviewing the manuscript. Anne Slobodchikoff was very helpful in editing and typing the manuscript.

TABLE 1. The source of variation in conifer seeds as a food resource.

Species	Source of units	Number	Range	Mean	Coefficient of variation
Caloric value of female gametophyte and embryo (Cal/g dry weight):					
Lodgepole pine	groups of 6 to 10 seeds from one cone	5	6.55-6.91	6.74	2.0%
Lodgepole pine	groups of 6 to 10 seeds from one tree	6	6.63-7.04	6.79	2.3%
Lodgepole pine	groups of 5 to 10 seeds from one population	7	6.54-6.96	6.83	2.2%
Weight of female gametophyte and embryo (mg/seed):					
Engelmann spruce	seeds from one cone	40	1.6-2.0	1.91	7.5%
Lodgepole pine	seeds from one cone	25	1.7-2.3	1.88	9.5%
Lodgepole pine	10 means of seeds from 10 cones from one tree	10	2.01-3.27	2.49	14.8%
Lodgepole pine	6 means of seeds from 6 cones from different trees	6	1.88-3.63	2.53	24.0%
Filled seed content of cones (filled seeds/cone):					
Lodgepole pine	cones from one tree	5	9-23	15.8	40.4%
Lodgepole pine	10 means of cones from 10 trees	10	4.4-18.8	11.6	39.5%
Ponderosa pine	cones from one tree	5	53-89	70.4	22.9%
Ponderosa pine	7 means of cones from 7 trees	7	39.0-70.4	53.5	20.6%
Annual cone crops (cones/tree or cones/acre):					
Douglas-fir	11 annual means for several trees (cones/tree)	11	0-14,244	4219	124.6%
Ponderosa pine	10 annual crops (cones/acre)	10	316-7521	2437	93.1%
Ratios of successive cone crops (%):					
Douglas-fir	smaller crop/larger crop $\times$ 100 for 10 pairs of successive years	10	0.0-67.2	6.9	
Ponderosa pine	smaller crop/larger crop $\times$ 100 for 9 pairs of successive years	9	4.2-94.4	40.2	
Lodgepole pine	smaller crop/larger crop $\times$ 100 for 4 pairs of successive years	4	50.8-73.5	62.4	

Family: Sittidae			
✓ White-breasted Nuthatch	<i>Pinus</i>	uses and makes cache of seeds and finds seeds on ground	alternate foods
✓ Red-breasted Nuthatch	<i>Abies, Picea, Pinus, Pseudotsuga, Tsuga</i>	seeds from open cones cached and eaten by adults	alternate foods, emigration
✓ Tyngy Nuthatch	<i>Abies, Picea, Pseudotsuga, Pinus</i>	seeds from open cones cached and eaten by adults	alternate foods
Family: Ptingillidae			
✓ Crossbills	<i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	seeds from closed and open cones fed to young and adults	nomadic nesters, emigrate to alternate foods
✓ Pine Siskins	<i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	seeds from open cones and the ground fed to young and adults	emigration, alternate foods
genus: <i>Canutus</i>			
MAMMALS:			
Order: Rodentia			
pine squirrels	<i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	cache and feed from whole closed cones	territoriality, emigration, alternate foods
genus: <i>Tamiasciurus</i>	<i>Pinus</i>	seeds from closed cones	alternate foods
tree squirrels			
genus: <i>Sciurus</i>	<i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	cache and eat seeds from closed or open cones	alternate foods
chipmunks	<i>Pinus</i>	forage for single seeds	alternate foods
genus: <i>Eutamias</i>			
golden-mantled ground squirrel			
<i>Spermophilus lateralis</i>			
deer mice	<i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	forage for single seeds and cache seeds	alternate foods
genus: <i>Peromyscus</i>	<i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	forage for single seeds and cache seeds	alternate foods
red-backed voles			
genus: <i>Clethrionomys</i>			
Order: Insectivora			
shrews	<i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>	forage for single seeds	alternate foods
genus: <i>Sorex</i>			

TABLE 3. *continued*

Taxonomic group of seed predators	Genera of trees exploited	Method of conifer exploitation	Method of escaping starvation during cone crop failure
BIRDS:			
Family: Psittacidae parrots Genus: <i>Rhynchopsitta</i>	<i>Pinus</i>	extracted seeds from closed and open cones	emigration, nomadic
Family: Picidae ✓ Hairy Woodpecker White-headed Woodpecker Genus: <i>Picoides</i>	<i>Pinus</i>	extracted seeds from closed and open cones eaten by adults and juveniles	alternate foods
Family: Corvidae ✓ Pileated Jay Genus: <i>Gymnorhinus</i>	<i>Pinus</i>	cache seeds extracted from closed and open cones to feed young and adults	alternate foods, emigration
✓ Clark's Nutcracker Genus: <i>Nucifraga</i>	<i>Pinus</i>	cache seeds extracted from open and closed cones to feed young and adults	alternate foods, emigration
✓ Gray Jay Genus: <i>Perisoreus</i>	<i>Abies, Picea</i>	may extract seeds from open cones or retrieve from ground to eat and store as hoard	alternate foods, territorial
✓ Steller's Jay Genus: <i>Cyanocitta</i>	<i>Pinus</i>	cache seeds from open cones to feed adults	alternate foods, territorial, emigration
Scrub Jay Mexican Jay Genus: <i>Aphelocoma</i>	<i>Pinus</i>	cache seeds from open cones and ground to feed adults	alternate foods, territorial
✓ Black-billed Magpie Genus: <i>Pica</i>	<i>Pinus</i>	cache seeds from open cones and ground to feed adults	alternate foods, territorial
Family: Paridae ✓ Mountain Chickadee	<i>Abies, Picea, Pseudotsuga, Pinus</i>	cache seeds from open cones and ground to feed adults	alternate foods
Boreal Chickadee	<i>Abies, Picea, Pseudotsuga</i>	cache seeds from open cones and ground to feed adults	alternate foods
Plain Titmouse Genus: <i>Parus</i>	<i>Pinus</i>	cache seeds from open cones and ground to feed adults	alternate foods, territorial

Talking Points

Noted

■ Americans who get health insurance through the Affordable Care Act will see their monthly premiums jump an average of 75% next year, according to an analysis by the non-partisan Kaiser Family Foundation. The rise is largely due to the end of Covid-era enhanced subsidies, which started under the Biden administration and helped ACA enrollment more than double to a record 24 million people. [NPR.org](https://www.npr.org)

■ The Trump administration has been accused of resisting court orders in a third of the more than 160 major judicial rulings against it. Plaintiffs say administration lawyers have defied rulings, provided false information, and failed to turn over evidence. Judges have often agreed, but none have taken punitive actions to force compliance. *The Washington Post*

■ Millions of travelers to the U.S. will soon have to pay a \$250 "visa integrity fee" to enter the country. The fee, included in the Trump admin-



istration's recently passed megabill, will apply to visitors who need non-immigrant visas, including tourists, foreign students, and business travelers. The fee is refundable, but the law doesn't specify how visa holders can apply for reimbursement or how the fee will be collected. [CBSNews.com](https://www.cbsnews.com)

■ The National Weather Service issued a record 3,040 flash-flood warnings from Jan. 1 through July 15, more than any other year for that time period since 1986, when the modern alert system was adopted. In early July, the U.S. experienced at least four 1-in-1,000-year downpours in less than a week. [NBCNews.com](https://www.nbcnews.com)

Kiss cam: When love cheats go viral

It's "hard to imagine a more surreal or absurd scene" than last week's viral incident at a Coldplay concert outside Boston, said Kat Rosenfield in *The Free Press*. As captured on an audience member's cellphone and shared on TikTok, the stadium's "kiss cam" landed on a middle-aged couple in a swaying embrace, whose blissful smiles abruptly turned to "looks of sheer panic" as they saw themselves on the jumbotron. "Either they're having an affair,"

Coldplay frontman Chris Martin told the crowd, "or they're just very shy." Internet sleuths understood what to do next: Seemingly within minutes, they'd outed the pair as Andy Byron, the married CEO of software startup Astronomer, and Kristin Cabot, the firm's also married head of HR. Then came a "tidal wave" of spoofs, joke memes, and merch—one Etsy seller is hawkking a T-shirt with the slogan "I Took My Sidepiece to the Coldplay Concert and It Ruined My Life." Byron soon resigned. It was a dismal orgy of "public shaming," with a gleeful mob feeding on the "ruination" of people felled by "terrible luck and atrocious judgment."

The "morality police" are impossible to escape in the internet age, said Tatum Hunter in *The Washington Post*. Between kiss cams, Ring doorbells, omnipresent surveillance systems, and a cellphone in every pocket, "the cameras are always rolling."



Before the panic set in

a question: "When did America get this cruel?"

"Schadenfreude" plays a role here, said Chip Cu and Lauren Weber in *The Wall Street Journal*. The kiss cam vid blew up in part because the pair were top tech executives at a time of "simmering frustration toward the executive class." And given HR-enforced policies about office romances and "power imbalances among co-workers," the irony and hypocrisy were hard to miss. It was a sordid affair, said Helen Schulman in *The New York Times*, but an oddly "refreshing" one. In our era of "shamelessness," with a blame-dodging president convicted of 34 felony counts sitting in the Oval Office, it was "a strange relief" to watch two people face the consequences of their actions. For brief moment, the concept of shame was "brought back from the dead," and that seemed like "something to celebrate."

Bove: The start of a MAGA judiciary?

Senate Republicans are poised to confirm "one of the worst judicial nominations ever," said Jackie Calmes in the *Los Angeles Times*. The chamber's GOP-led Judiciary Committee voted last week to advance the nomination of Emil Bove—President Trump's former personal attorney "and for the past six months his enforcer in the Justice Department"—to a lifetime post on a federal appeals court. Democrats stormed out of the vote after the panel's chair, Chuck Grassley (R-Iowa), refused to let some of them air objections or to hear from a whistleblower who alleged that Bove told Justice Department lawyers they'd need to consider saying "F--- you" to judges who block Trump's deportation agenda. That's not the only time Bove, 44, has shown utter contempt for the law: He engineered the pardons of Jan. 6 insurrectionists and the purge of DOJ lawyers who worked their cases, and forced through the dismissal of corruption charges against New York City Mayor—"and sometimes Trump ally"—Eric Adams. Bove is "not merely unqualified to be a judge but disqualified." Yet his nomination is likely to meet little resistance from Trump-fearing Republicans when it reaches the Senate floor.

"The concerns about Bove's nomination aren't frivolous," said *The Wall Street Journal* in an editorial. The former federal prosecutor hasn't exactly

denied the whistleblower's allegations, saying merely that he didn't recall dropping the f-bomb and that at the time there were "no court orders to discuss" or consider violating. Then there's his nixing of Adams' prosecution, on the grounds that the case was hampering the mayor's cooperation with Trump's migrant crackdown, "an implicit quid pro quo" that led to a series of resignations at the DOJ. Bove clearly has a talent for "pushing legal boundaries," but that's not a desirable quality in a judge.

As a former district attorney, I can't "recall such fierce and widespread opposition" to a nomination, said Mimi Rocah in *MSNBC.com*. More than 900 former DOJ attorneys and 75 retired judges from across the political spectrum have written the Senate to oppose the confirmation of Bove, who has shown he cannot be trusted "to uphold the Constitution and act with integrity." That's exactly why Trump wants Bove and others like him on the bench, said Jeffrey Toobin in *The New York Times*. The president has griped that the three conservative Supreme Court justices he appointed in his first term have not sufficiently stood behind his agenda. That wouldn't be a problem with Bove, who has "proved that he belongs to the president" and who Trump is now likely "grooming for bigger things"—including a possible high court seat.

Forest
Service

Northern
Region



Old-growth Habitats and Associated Wildlife Species in the Northern Rocky Mountains

1990

Marten

$200/10,000 = 2\%$

$500 = 5\%$



1990-1991

OLD-GROWTH HABITATS

Inventory and Stand Selection

WILDLIFE SPECIES ASSOCIATED WITH OLD-GROWTH HABITATS

Meslow and Wight (1975) found that 69 percent of the birds occurring in Douglas-fir forest types of the Pacific Northwest used old-growth stands. Three species were listed as nesting primarily within old-growth forests: spotted owl, northern goshawk, and Vaux's swift. Bull (1978) identified six species which are primarily associated with old-growth forests in Oregon: great gray owl, barred owl, flammulated owl, white-headed woodpecker, northern three-toed woodpecker, and Townsend's warbler. The marten is associated with mature and old-growth spruce-fir forests in Idaho (Koehler and Hornocker 1977).

In northwestern Montana, McClelland (1977) described a general trend of increased species richness in cavity-nesting birds from young to old-growth stands of larch and Douglas-fir. Old growth was particularly important in providing an adequate number of suitable nesting trees for cavity-nesters. He also noted the association of open-nesters such as the pine grosbeak, Townsend's warbler, varied thrush, black-headed grosbeak, and goshawk with old-growth forests, as well as its value as big game thermal cover.

Based on a literature review, about 40 percent of the 373 wildlife species occurring in the Northern Region were thought to use old-growth forest for feeding and/or reproduction (Harger 1978). Of these, 33 species were thought to be closely associated with old-growth habitats (Table 1).

The following describes the importance to wildlife of various components of old-growth habitats.

Overstory Trees. Large trees are needed to provide suitable nesting sites for large birds. Bark crevices in older trees provide

important foraging sites. Large-canopied trees can modify microclimate by providing shade, capturing moisture, and moderating winds.

Dead and Defective Trees. Dead trees (snags) and defective trees (partially dead, spike top, broken top) provide nesting and roosting sites for cavity-users. Snags host invertebrates which are an important food source for woodpeckers.

Down Woody Material. Downfall supports insects and other invertebrates, provides habitat for fungi and saprophytic plants, provides cover and den sites for wildlife, and creates debris dams in streams. Dead woody material holds moisture and contributes to nutrient cycling. In areas with high frequency of fire, this component will be less abundant.

Tree Canopy. A relatively closed canopy, often with two or more layers, creates a more moderate microclimate. Vertical diversity provides a variety of substrates for feeding or nesting, and supports development of forest components such as arboreal lichens.

Decadence. Presence of heart rot, mistletoe, dead or broken tree tops, diseased trees, and saprophytic plants create a variety of microsites and food sources for wildlife.

MANAGEMENT INDICATOR SPECIES

The National Forest Management Act and its implementing regulations require that fish and wildlife habitats be managed to maintain viable populations of existing native and desired non-native vertebrate species in the planning area. In order to estimate the effects of each Forest Plan alternative on fish and wildlife populations, Management Indicator Species (MIS) are to be selected.

OLD-GROWTH HABITATS
Inventory and Stand Selection

Table 1. Species in the Northern Region (north Idaho, Montana, North Dakota, and South Dakota) thought to prefer old-growth components for breeding or feeding (from Harger 1978).

WILDLIFE SPECIES	STRUCTURAL STAGES		OPTIMUM COVER TYPE
	Breed	Feed	
Great Blue Heron	5-6	1	ASP, COT
109 Northern Goshawk	5-6	3-6	ASP, DF, PP, LPP
109 Great Gray Owl	6	1	LPP, SAF, SP
Flammulated Owl CN	5-6	1-2	PP, DF, GF, LPP
Pygmy Owl CN	5-6	1-6	PP, DF, GF, WL
Saw-whet Owl CN	5-6	1-6	PP, DF, GF, LPP, SAF, SP
Boreal Owl CN	5-6	1-6	PP, ASP, SP, SAF, DF
Barred Owl CN	5-6	3-6	COT, DF, GF
Vaux's Swift	5-6	1-6	ASP, COT, DF, WRC
White-headed Woodpecker CN	4-6	4-6	PP, WWP
✓Pileated Woodpecker CN	4-6	3-6	COT, PP, WL, GF
Three-Toed Woodpecker CN	4-6	3-6	SAF, WBP
Black-backed Woodpecker CN	4-6	3-6	PP, DF, WWP
Red-naped Sapsucker CN	4-6	1-6	BGA, COT
Williamson's Sapsucker CN	4-6	2-6	PP, WL, GF, SAF, SP
White-breasted Nuthatch CN	4-6	3-6	PP, DF
✓Red-breasted Nuthatch CN	4-6	3-6	PP, ASP, LPP, SAF, SP
Pygmy Nuthatch CN	4-6	3-6	PP, DF
✓Brown Creeper CN	4-6	3-6	DF, LPP, SP, SAF
Great Crested Flycatcher	4-6	2-4	BGA, COT
✓Hermit Thrush	5-6	2-6	GF, WH, WRC, SAF, SP
✓Varied Thrush	5-6	2-6	WH, WRC, SP
✓Townsend's Warbler	4-6	2-6	ASP, COT, PP, DF
Silver-haired Bat CN	3-6	1-3	PP, DF, WRC, SP
Long-eared Bat CN	4-6	1-6	PP, DF, GF
Long-legged Myotis	4-6	1-6	LPP, SAF, SP
California Myotis	4-6	1-6	BGA, COT, PP, JPU
109 Fisher	5-6	3-6	ASP, COT, PP, DF, WWP
109 Marten	5-6	2-6	LPP, SAF, SP, WRC
109 Wolverine	3-6	1-6	SAF, WBP
Woodland Caribou	5-6	5-6	SAF, SP, WH, WBP
109 Boreal Red-back Vole	4-6	4-6	SAF
Northern Flying Squirrel CN	5-6	5-6	ASP, COT, DF, WWP, SAF

Structural Stages: 1=Grass/Forb, 2=Shrub/Seedling, 3=Pole Trees, 4=Young Trees, 5=Mature Trees, 6=Old-Growth

Cover Types: ASP=Aspen, BGA=Birch/Green Ash, COT=Cottonwood, DF=Douglas-fir, GF=Grand Fir, JPU=Juniper, LPP=Lodgepole Pine, LP=Limber Pine, PP=Ponderosa Pine, SAF=Subalpine Fir, SP=Spruce, WH=Western Hemlock, WL=Western Larch, WRC=Western Redcedar, WWP=Western White Pine, WBP=Whitebark Pine

OLD-GROWTH HABITATS

Inventory and Stand Selection

Several categories of species are to be represented where appropriate: Endangered and threatened plant and animal species; species with special habitat needs that may be influenced significantly by planned management programs; species commonly hunted, fished or trapped; non-game species of special interest; and plant or animal species selected because their population changes are believed to indicate the effects of management activities on other species of selected major biological communities (36 CFR 219.19). The first four categories of MIS include "featured species", wherein management activities are directed to providing specific habitat components to meet management objectives for the individual species. The latter category is intended to include ecological indicators, which are selected to represent a larger community of species.

An ecological indicator will ensure the welfare of only those species whose niches are entirely included within its habitat niche and geographic range. To be effective, then, an ecological indicator should have a large home range and be closely associated with a specific habitat.

The goshawk, pileated woodpecker, and marten were identified as MIS by most Forests in the Northern Region to be used as ecological indicators for old-growth components or old-growth habitats. Each of these species have habitat requirements related to stand structure or components which are more likely to be found in old-growth habitats. Their population densities generally are higher in old-growth than in younger stands. In a California study, both marten and pileated woodpecker were found to be sensitive to habitat fragmentation (Rosenberg and Raphael 1986). Each of these species utilize a relatively large home range, which is thought to include the home ranges of other old-growth-associated species.

The habitat requirements of pileated woodpecker, goshawk, and marten, and models for assessing habitat suitability for each are detailed in subsequent sections. Although

Schroeder (1987) identified several problems in HSI modeling, they are the most expedient method for evaluating impacts of habitat change.

The requirements of these species in terms of the size and spacing of habitat patches can be used to determine the distribution of old-growth habitats across the landscape.

OLD-GROWTH STAND SELECTION

Landscape Ecology Theory. Forman and Godron (1981) defined landscape patches as communities surrounded by a matrix with a dissimilar community structure or composition. They hypothesized that species diversity within a patch is a function of habitat diversity, disturbance, area, age, surrounding heterogeneity, isolation, and boundary discreteness.

Old-growth habitats offer comparatively high within-stand structural diversity. As forest management progresses through time, old-growth forests will be represented as remnant patches embedded in a younger-aged matrix.

Patch size correlates strongly with the numbers of species and individuals that can be supported and with rates of extinction and recolonization (May 1975, Simberloff and Aberle 1982). Patch size is particularly significant for large, wide-ranging species (Noss and Harris 1986). As acreage decreases, habitat patches become unsuitable for wildlife species with large home ranges. Of 48 old-growth-associated species occurring in the Northern Region, about 60 percent are thought to require stands larger than 80 acres (Harger 1978).

Patch size is modified by its shape due to edge effect. Changes in temperature, humidity, light, and wind, which influence plant species composition, can occur in a band along the ecotone (edge) (Greene 1988). In Douglas-fir old-growth forest, a circular-shaped stand smaller than 25 acres is effectively all "edge" (influenced by the ecotone); within a stand of 80 acres, half of

OLD-GROWTH HABITATS Inventory and Stand Selection

the patch provides "interior" conditions (Lemkuhl and Ruggerio in prep.). In northern California, Rosenberg and Raphael (1986) found that old-growth Douglas-fir stands of less than 50 acres tended to lack the full complement of vertebrate wildlife, and suggested that isolated stands should exceed 125 acres in size to be effective. Wilcove et al. (1986) estimated that habitat islands should exceed 250 acres to provide for birds inhabiting forest interior.

The abruptness of the edge, or edge contrast, affects stand insularity. Edges between similar cover types and successional stages cause less isolation than do edges between very dissimilar stands. A patch totally surrounded by dissimilar habitat becomes more similar to a true island, with less movement of species between patch and matrix (Forman and Godron 1981).

Selection of Stands to Manage for Old-Growth Conditions. The recommended scale for initial analysis of the quality and distribution of existing old-growth habitats is the watershed scale (typically about 10,000 acres in size). Individual stands or groups of contiguous stands can be evaluated using a scorecard method. The habitat requirements and dispersal capabilities of old-growth Management Indicator Species should be used to determine the size, shape and spacing of old-growth patches across the forest landscape.

If a particular analysis unit does not contain existing stands of high quality, large enough size, or sufficient overall acreage, the best available (nearest to old-growth condition) stands should be selected. Alternatively, old-growth stands in adjacent watersheds could be selected, provided the spacing of old-growth patches does not exceed the mobility of the MIS.

Roads are generally undesirable within an old-growth habitat patch. The road corridor fragments the habitat by creating edge, and access may result in loss of snags to woodcutting.

Landres et al. (1988) point out that selecting old-growth stands based on within-patch habitat conditions required by the MIS, and then predicting or monitoring habitat conditions for those MIS, is circular reasoning. Because old-growth-associated MIS are intended to represent a community of wildlife species, stand selection and management should not be directed only towards providing the minimum characteristics required by the individual species. Management objectives and actions in the selected old-growth patches should be directed towards protecting or enhancing the integrity and longevity of old-growth conditions.

In devising a conservation strategy, Forman and Godron (1981:738) emphasize the importance of recognizing that "no patch stands alone", but is influenced by surrounding patches. Harris (1984) recommended surrounding old-growth habitat islands with a long-rotation management area, and interconnecting these with riparian corridors and other linkages. Similarly, Noss and Harris (1986) suggest that a regional landscape level be used, wherein high-quality nodes, such as an old-growth patch, would be integrated within interconnected "multiple-use modules", where management activities are scheduled to maintain the integrity of the nodes.

Natural disturbance regimes such as fire often occur on a spatial scale larger than a landscape patch (Urban et al. 1987). Providing for well-distributed habitat patches with interconnections between patches thus are necessary to maintain species diversity over the long term.

OLD-GROWTH HABITATS

Goshawk

Goshawk nesting territories include 2-5 nest trees. Alternate nests can usually be found within 325 feet (100 m) of each other, and are almost always within 0.6 mile of each other (Reynolds 1975). Previously-used nest trees are often re-used, even if the nest is no longer intact or evident.

Nest Stands. Throughout western North America, goshawk nest stands consistently have been described as mature to old-growth (Reynolds 1978, Hennessy 1978, Hall 1982, Saunders 1982, Hayward 1983).

The mean canopy cover of 80 percent (measured with spherical densiometer or on aerial photos) surrounding 17 nests in the northern Rockies (Hayward 1983) was very similar to nest sites in northeastern Oregon (Moore 1980), California (Hall 1982), and Arizona (Crocker-Bedford and Chaney 1988). In Utah (Hennessy 1978), canopy cover averaged 63 percent, and in Oregon 61 percent (Reynolds et al. 1982).

Forest stands selected for nesting may be either multi-storied or single-storied, with a relatively open understory (Schnell 1958, Dietzen 1978, Hennessy 1978, Shuster 1980, Hall 1982, Reynolds et al. 1982). Dense understory is believed to make a stand less suitable by inhibiting goshawk flight and providing escape cover for prey species (Reynolds 1978). In the northern Rockies, both single and multi-storied stand structures were used by nesting goshawks (Hayward 1983).

Relatively high basal areas have been recorded at goshawk nest sites in Arizona, California, and Oregon (Moore 1980, Hall 1982, Crocker-Bedford and Chaney 1988). In the northern Rockies, 60 percent of 17 nest stands had basal areas between 160 and 190 ft²/acre (Hayward 1983).

Goshawk nest stands generally would be considered fully stocked, with moderate to high tree density (Moore 1980, Reynolds et al. 1982, Hall 1982). In the northern Rockies, nest stands had an average of 454 trees/acre larger than 3 inches dbh (Hayward 1983).

Goshawks appear to select nest sites on gentle to moderately steep slopes. In the northern Rockies, slopes of nest stands range from 2-45 percent (average 27 percent), with over 70 percent of nests occurring on the lower one-third or bottom of the slope (Hayward 1983).

Goshawk nests have been reported to occur most frequently on northerly aspects in Utah, Oregon, and California (Hennessey 1978, Reynolds et al. 1982, Hall 1982). In Arizona, Crocker-Bedford and Chaney (1988) found that nests in ponderosa pine types were on northerly aspects, while no difference was observed in mixed conifer forests. In Alaska, nests were found on southerly aspects (McGowan 1975).

Food Habits. Prey items between 200 and 400g appear to be optimum as indicated by mean prey size (Storer 1966, Reynolds 1978, Wikman and Linden 1981). Tree squirrels, ground squirrels, woodpeckers, grouse, jays, and robins are important prey species.

Avian prey items occurred more frequently than mammalian prey in eastern Oregon (54% birds, 42.7% mammals; Reynolds 1978), and in the Sierra Nevada of California (77% birds, 23% mammals; Schnell 1958). Mammalian prey was more important by both number and volume (biomass) in the Coast Range of California (Woodbridge et al. 1985).

Foraging Habitat. The short, rounded wings and long tail of *Accipiter* hawks enables the birds to perform rapid wheeling flights over short distances. Reynolds (1978) indicated that goshawks forage predominantly in the ground-shrub and shrub-canopy zones in forested situations.

Forest habitat, pole stage or larger, which is open enough to allow the goshawk unimpeded flight through the understory, is considered completely suitable for foraging. "Doghair" stands with more than 750 trees/acre, larger than 3 inches dbh, are considered unsuitable foraging habitat (Hayward et al. 1983).

OLD-GROWTH HABITATS

Goshawk

Observations suggest that goshawks hunt forest edges and openings, in addition to hunting within moderate to densely forested stands (Craighead and Craighead 1956, Schnell 1958, Wattel 1973, Fox 1981). Openings are considered fully suitable if all portions of the opening are within 100 yards of an edge; portions of an opening over 500 yards from forest are thought to be unsuitable (Fox 1981). *

In Arizona, Crocker-Bedford (pers. comm.) found that goshawk nestling production decreased by 95% following partial cutting, despite leaving buffers averaging 95 acres (range 40-500 acres) around the nests. The harvesting was believed to have adversely affected prey production and availability, and increased competition from Red-tailed Hawks and Great Horned Owls.

Goshawks used plucking posts to dismember and consume prey. Large-diameter snags and stumps are frequently used for this purpose.

Water. Goshawks have been observed bathing during warm weather (Hennessy 1978). Shuster (1980) and Reynolds et al. (1982) suggested that sites near water are preferred for nesting. Open water and moist forest conditions may provide needed protection from heat and sunlight.

Water is not considered to be a limiting factor in boreal coniferous forests of western Montana or northern Idaho. In eastern Montana and in the Dakotas, water availability could be limiting.

Interspersion. Spring-summer goshawk habitat must contain forest stands with suitable structure for nesting, and adjacent foraging habitat with sufficient prey to raise a brood.

In western Montana and northern Idaho (the northern Rockies), over 50 percent of 17 nest sites surveyed were within 0.25 mile of a forest opening (Hayward 1983). However, it was not determined whether these nests occurred near openings through actual nest site selection, or merely reflected typical patterns of vegetation.

Home Range Size. Goshawk territories in the western U.S. have been found 1 to 4 miles apart (Shuster 1976, Dietzen 1978, Hall 1982, Crocker-Bedford and Chaney 1988). In Oregon, Reynolds (1975) measured the average distance between active nest territories as 2.7 miles.

Estimates of breeding population density vary widely. In the western U.S., density estimates range from one pair per 525 acres in Wyoming (Craighead and Craighead 1956); to one per 2,200 acres in Arizona (Crocker-Bedford and Chaney 1988); to one per 3,325 acres in Colorado (Shuster 1976); to one per 6,796 acres in Oregon (Reynolds and Wight 1978).

Dispersal Distance. No data documenting the dispersal distances of juveniles were found.

Marten Habitat Relationships

Tim Patton and Ron Escano

Revised by Nancy Warren

INTRODUCTION

The marten (*Martes americana*) was selected by many of the National Forests in the Northern Region as a Management Indicator Species. It was used to represent species using mature and old-growth habitats, particularly the down woody component.

The following describes the habitat relationships of the marten and a model which provides an index rating of the value of habitat for marten.

ECOLOGY OF THE MARTEN

Distribution. Marten inhabit late successional coniferous forests throughout northern North America in the Canadian and Hudsonian life zones (Marshall 1951, Hagmeier 1956, Strickland et al. 1982). In the western U.S., marten are most abundant in mature to old-growth true fir or spruce-fir forests and generally avoid open, xeric coniferous forests (Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Spencer 1981). The marten is generally nocturnal, and is active throughout the year.

Reproduction. Female marten do not mate until their second year. Litter size ranges from one to four, and kits are whelped in April (Brassard and Bernard 1939). Males do not care for the young.

Denning Habitat. Marten require large snags, stumps, and logs for resting sites and natal dens (Simon 1980, Spencer 1981). Wynne and Sherburne (1984) found that two females with kits used cavity dens until the kits were about eight weeks old; ground logs then were used until the kits were nearly adult size (12-15 weeks).

Food Habits. Microtines, especially red-backed voles (*Clethrionomys gapperi*) and meadow voles (*Microtus pennsylvanicus*), are used more than any other single food item (Cowan and Mackay 1950, Lensink et al. 1955, Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Soutiere 1979). Red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), and snowshoe hare (*Lepus americanus*) may also be important winter prey (Marshall 1946). In a Montana study, small mammals were the most important food item on an annual basis, with the highest utilization of mammalian prey occurring during the winter months; invertebrates, berries, and passerine birds were the most frequent food items recorded from spring through fall (Weckwerth and Hawley 1962).

Weckwerth and Hawley (1962) believed that fluctuations in small mammal densities in Montana directly affected the carrying capacity of an area for marten. Mech and Rogers (1977) suggested that food availability may be the most important factor limiting marten populations. Thompson and Colgan (1987) found that marten home range sizes were inversely related to food supply.

Feeding Habitat. Koehler and Hornocker (1977) found that mesic coniferous habitat types supported the greatest numbers of rodents. These habitat types therefore would be expected to have high value as marten foraging habitat.

Campbell (1979) reported that winter hunting was confined to dense stands of mature coniferous forest. In Wyoming, Idaho, and Colorado, highest marten activity was recorded in the spruce-fir zone (Yeager and Remington 1956, Koehler and Hornocker 1977, Buskirk et al. 1989). Lodgepole

OLD-GROWTH HABITATS

Marten

pine stands are used for foraging, if in proximity to old-growth stands (Spencer et al. 1983). In Washington, marten prefer Douglas-fir, cedar and hemlock types, while cedar swamps were frequented more than any other type in Ontario (deVos and Guenther 1952).

In general, marten prefer forest stands with greater than 40 percent tree canopy closure, and avoid those with less than 30 percent (Koehler and Hornocker 1977, Spencer 1981). Stands with less than 30 percent overhead cover, while used very little, were more likely to be used when snow depths were less than 12 inches (Koehler et al. 1975). Overhead cover provides marten with protection from predators, as well as enhancing the mesic conditions favorable for production of voles.

Marten rarely venture more than 150 feet from forest cover, especially in winter (Koehler and Hornocker 1977, Hargis 1981, Spencer 1981). Koehler and Hornocker (1977) believe that openings, which are avoided in the winter, may be used for summer and fall foraging if adequate food and cover are present. Female marten are less likely to cross open areas than are males (Steventon and Major 1982).

Clark and Campbell (1976) suggested that marten winter densities may be limited more by access routes to get at prey below deep snow than the actual density of rodents present. During winter, trees, logs, slash, etc., projecting above the snow provide marten with access to rodents dwelling below the snow (Koehler et al. 1975, Soutiere 1979).

Resting Habitat. Resting sites are usually beneath forest canopy (Simon 1980, Spencer 1981). Closed canopy forest creates a favorable microclimate by reducing snow depth and providing insulation from cold winds. Spruce-fir cover types were preferred resting sites in Wyoming (Raphael pers. comm.).

Large down logs and stumps are especially important in winter for thermal cover (Buskirk

et al. 1989). Winter resting sites typically are found under the snow layer, under stumps, snags or logs, and often in squirrel middens (Marshall 1951, Spencer 1981, Steventon and Major 1982, Buskirk 1984).

Water Requirements. The marten's physiological requirements for water remain unknown. Marten concentrate their foraging activities in mesic habitats and near water, probably because of its effects on vegetation structure and prey abundance (Koehler and Hornocker 1977, Spencer 1981).

Security. Marten are easily trapped and are susceptible to overharvest (Soutiere 1979). The effects of road density on marten have not been quantified. Particularly when roads are located through marten travel corridors (ridges, saddles, and riparian zones) and foraging areas, increasing road access is thought to increase the vulnerability of marten to trapping (M. Frisina, pers. comm.).

Home Range Size. Population densities of marten in good habitat generally average about 1 to 3 per square mile (Burke 1982). Home ranges of resident males are distinct, but female home ranges often overlap other female and male ranges (Clark and Campbell 1976, Powell 1979, Burnett 1981).

In Glacier National Park in Montana, mean home range size was estimated to be about 1.0 square mile for resident males and 0.27 square miles for resident females (Hawley and Newby 1957, Burnett 1981). Similar home range sizes were reported in Wyoming (Clark and Campbell 1976). Larger home range sizes have been reported in other areas: for example, Wyoming, 10 square miles for males and 6 for females (Raphael pers. comm.); Minnesota, 6 square miles for males and 1.7 for females (Mech and Rogers 1977); Maine, 3.5 square miles for males and 0.9 for females (Steventon and Major 1982); and California, 1.4 square miles for males and 1.2 for females (Simon 1980, Spencer 1981).

Buskirk and McDonald (*in press*) analyzed variability in home range size as determined

by radiotelemetry in 9 separate areas. Home range size varied significantly between the 9 study sites, but showed no obvious geographic pattern (latitude, longitude, elevation, or mean annual temperature range). Mean home range sizes (1160 acres for adult females and 1750 for adult males) are about 3 times that predicted for terrestrial carnivores based on body mass (Linstedt et al. 1986).

Soutiere (1978) reported that home ranges were larger in clearcut forests than in uncut or partially cut forests. Similarly, in Ontario Thompson and Colgan (1987) found that home range sizes were larger in cutover than in uncut forest, and increased during years of scarce food supply. Home range sizes in uncut sites varied from 1.21 to 2.45 square miles for males and from 0.36 to 1.53 square miles for females in years of abundant and scarce food availability, respectively.

Marten home ranges must include resting areas and foraging areas, with adequate cover in close proximity. Marten home range boundaries often coincide with edges of topographic or vegetative features such as large open meadows, burns, or streams (Hawley and Newby 1957).

Dispersal Distances. The dispersal capabilities of marten are not well known, but juveniles have been observed to travel up to 24 miles in order to become permanently established in an adequate home range (Hawley 1955). Jonkel (1959) recorded juvenile movements averaging 9.7 miles for seven males (range 2-25 miles) and 7.5 for four females (range 2-15 miles). An average maximum movement of 6.3 miles was observed by Burnett (1981) for two male and one female non-resident juveniles.

Pileated Woodpecker Habitat Relationships

William C. Aney and B. Riley McClelland

Revised by Nancy Warren, Karen Wilson, Mike Hillis, Bob Summerfield,
Carl Frounfelker, Tom Wittinger, and Wally Murphy

INTRODUCTION

The pileated woodpecker requires tall, large-diameter dead or live defective trees within forest stands for nesting. It is particularly characteristic of old-growth stands of ponderosa pine, western larch, and black cottonwood stands.

Most of the Forests in the Northern Region have selected the pileated woodpecker as a Management Indicator Species for old-growth habitats. The following describes habitat requirements of the pileated woodpecker, a model to evaluate habitat suitability, and recommended methods for inventory and monitoring of habitats and populations.

ECOLOGY OF THE PILEATED WOODPECKER

Distribution. The pileated woodpecker (*Dryocopus pileatus*) is a year-round resident of forested areas in the northern Rockies. This large woodpecker is absent from the central and southern Rockies (Bent 1964), probably due to the absence of dense highly productive forests in those regions (Bock and Lepthien 1975).

Reproduction. Courtship usually begins in mid-March. Both drumming and vocalizations are used by the male to attract a mate. Pileateds regularly begin breeding as one-year olds, and virtually all birds breed every year (Bull 1987).

One or more new cavities are excavated during courtship each year, within the heartwood of a tree. The distance between successive nests used by the same pair

averaged 0.3 mile (0 - 1 mile) in Oregon (Bull 1987).

Clutch size is typically four. The incubation period, usually occurring in May, is about 18 days. The nestlings fledge about one month after hatching. Usually 2-3 young fledge from a nest.

Birds that were banded as nestlings and later nested within the same study area in Oregon (Bull 1987) dispersed an average of two miles (0 - 5.2 miles).

Nesting Habitat. Typical pileated nest stand conditions can best be described as old-growth stands with a decadent overstory of western larch, ponderosa pine, black cottonwood, or aspen. Stands of 50 to 100 contiguous acres, generally below 5000 feet in elevation, with basal areas of 100-125 square feet per acre and a relatively closed canopy, were used for nesting (McClelland 1977, 1979a, Bull 1980). The grand fir cover type was preferred in Oregon and western larch/Douglas-fir cover types are preferred in Montana (Bull 1987, McClelland et al. 1979).

Nests in the northern Rocky Mountains most commonly occur in dead ponderosa pine, dead black cottonwood, or live or dead western larch trees. Nest trees average nearly 30 inches in diameter, and are more than 91 feet tall in Montana (Aney and McClelland 1985). Minimum nest tree diameter is 20 inches dbh. Nest cavities usually are located more than 30 feet above the ground, at a level within the canopy of the surrounding forest (McClelland 1979a, Bull 1980).

OLD-GROWTH HABITAT Pileated Woodpecker

Heart rot appears to be an important feature of suitable nest trees. Decay fungi (*Lariciformes laricis* or *Phellinus pini*) enter the heartwood of living or dead larch trees through a broken top, fire scar, or other wound; decay gradually softens the heartwood while leaving a shell of sound sapwood. Conner et al. (1976), McClelland (1977, 1979a), Mannan et al. (1980), and Harris (1983) all reported a high incidence of broken tops in nest trees.

Pileated woodpeckers are able to excavate cavities in sound wood, however. Bull (1975, 1980) reported that the majority of nest trees in her northeastern Oregon study area, where ponderosa pine was the most common nest tree, showed no evidence of decay at the nest site. This apparently is related to characteristics of the dominant nest tree species of the two regions. Ponderosa pine was the most common nest tree in northeastern Oregon; western larch was predominant in the Montana study. Sound ponderosa pine, with a specific gravity of about 0.37 g/ml, is considerably softer than sound western larch (specific gravity of 0.48-0.52 g/ml). Decayed western larch heartwood, however, is softer than sound pine wood (0.27 g/ml) (McClelland 1977, Harris 1983).

In the Northern Region, either live or dead larch trees can be suitable nest trees, if heart rot is present. Ponderosa pine trees need not have decay at the nest site, but the excavated portion of the bole must be dead. Nest excavation in black cottonwood occurs almost always in dead portions of the bole, but the presence of heart rot is not essential (McClelland 1977). Aspen can provide suitable nest sites if trees are large enough.

Food Habits. Pileated woodpeckers feed principally on carpenter ants (*Camponotus herculeanus* and *C. pennsylvanicus*), excavating deep into ant colonies in dead and decaying wood (Sutton 1930, Bent 1964, Hoyt 1957, McClelland 1977, Bull 1980, Miller and Miller 1980). Beal (1911) examined the stomach of one pileated woodpecker and found the remains of more than 2600

ants. Estimates of the proportion of ants in the diet range from 40-60% (Koehler 1981) to 95% (Bull 1987).

Other insects reported in the diet include termites (Isoptera) and beetles (Coleoptera), which are obtained by bark gleaning, scaling, or excavating. In winter, when few insects are available on the boles of trees, pileateds feed principally by excavating.

Fruits and berries form a secondary component of the diet of pileated woodpeckers in the late summer and fall.

Feeding Habitat. Because carpenter ants make up the bulk of the pileated woodpecker's diet, suitable ant habitat is selected for foraging by pileated woodpeckers. These ant colonies occur most often in large snags with advanced decay, the moist decaying butts of live trees, logs greater than 10 in. in diameter, and natural or cut stumps (Cline 1977, Conner et al. 1975, Bull 1980, Bull and Meslow 1977, McClelland 1977, 1979a). Furniss and Carolin (1977) noted that carpenter ants especially favor fire-scarred and butt-rotted western redcedar trees, and will make extensive use of Douglas-fir, pines, and true firs.

In Montana, carpenter ants were found to select stands of high canopy cover, but ant densities declined as canopy cover increases past 90% (Youngs and Campbell n.d.). Similarly, stands with basal area in the range of 100 sq.ft. per acre were favored over more densely stocked stands (>150 sq.ft. per acre). *C.modoc* densities were positively correlated with dead wood volume in snags and stumps.

McClelland (1977) suggested that availability of food in winter may act as an ecological "bottleneck", limiting northern Rocky Mountain woodpecker populations. Snowpack makes logs and low stumps unavailable to feeding pileated woodpeckers.

McClelland (1979a) noted that pileated woodpeckers usually avoid open areas for feeding, preferring forests with a significant old-growth component and high basal

OLD-GROWTH HABITATS

Pileated Woodpecker

area. Shelterwood cuts and small group selection cuts are suitable, but not preferred, feeding areas. Bull and Meslow (1977) classified preferred feeding habitats as having high densities of snags and logs, dense canopies, and tall ground cover, with more than 10% of the ground area covered by logs. Kilgore (1971) found that reduction of dead and down woody material by fire caused a decline in the use of a giant sequoia forest by pileateds for feeding.

In the northern Rockies, the density of snags and stumps at pileated feeding sites (not throughout the feeding range) averaged 7 per acre (Aney and McClelland 1985). At least 500 acres of suitable feeding habitat is needed within the home range of a pair (McClelland 1979a).

Home Range Size. Nesting pairs of pileated woodpeckers in the northern Rockies often cover 500-1000 ac. in their daily feeding activities (McClelland 1979a). In high-quality

habitat in the northern Rockies, densities of 1 pair per 500 acres are not uncommon (McClelland pers. comm.). Bull (1987) estimated a density of one pair per 480 acres in northeastern Oregon, while Mellen (1987) reported an average home range size of 1200 acres for pairs in western Oregon.

Dispersal Distance.

Bull (1987) recorded juvenile dispersal distances of banded nestlings averaging 2 miles. The longest dispersal was 5.2 miles, although areas outside the study area were not searched, eliminating the chance of finding those that dispersed farther than 9.6 miles.

When adult birds lose their mates, they remain on territory. Juvenile dispersers are essential to mate with unpaired territorial adults and to recolonize unoccupied habitats (Bull pers. comm.).

REVISED FOREST PLAN
for the
TARGHEE NATIONAL FOREST
Intermountain Region R-4
April 1997

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Targhee National Forest
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Responsible Official:

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This Revised Forest Plan was prepared according to Secretary of Agriculture regulations (36 CFR 219), which are based on the Forest and Rangeland Renewable Resources Planning Act (RPA) as amended by the National Forest Management Act of 1976 (NFMA). This Revised Forest Plan was developed in accordance with regulations (40 CFR 1500) for implementing the National Environmental Policy Act (NEPA). A detailed Environmental Impact Statement (EIS) has been prepared as required by NEPA and 36 CFR 219.

If any particular provision of this Revised Plan, or the application of the action to any person or circumstances, is found to be invalid, the remainder of the proposed action and the application of that provision to other persons or circumstances shall not be affected.

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3. The following conditions and criteria will apply in determining the problem status of wolves. (USDI Fish and Wildlife Service 1994 a and b) (S)

A. Wounded livestock or some remains of a livestock carcass must be present with clear evidence that wolves were responsible for the damage and there must be a reason to believe that additional losses would occur if the problem wolf or wolves were not controlled. Such evidence is essential since wolves may simply feed on carrion they have found while not being responsible for the kill.

B. Artificial or intentional feeding of wolves must not have occurred. Livestock carcasses not properly disposed of in an area where depredations have occurred will be considered attractants. Removal or resolution of such attractants must accompany any control action. Livestock carrion or carcasses not being used as bait in an authorized control action (by agencies) must be removed, burned, treated with an acceptable chemical repellent, or otherwise rendered such that the carcass(es) will not attract wolves using methods approved by the District Ranger.

C. Animal husbandry practices previously identified in existing approved Allotment Management Plans and annual operating plans for allotments must have been followed.

4. If additional livestock depredations are likely, proper animal husbandry practices are employed (proper disposal of livestock carcasses, etc.), artificial feeding does not take place, and AMPs are followed, the Forest may implement procedures to harass, capture, move, or kill wolves that attacked livestock (defined as cattle, sheep, horses, or mules only) on National Forest land. (G) Prior to the establishment of six breeding pairs, depredating females and their pups will be captured and released at or near the site of capture, one time prior to October 1. If depredations continue, or if six packs are present, females and their pups will be removed. (USDI Fish and Wildlife Service 1994 a and b) (S)

Goal - Peregrine Falcon Habitat

Plan project activities to avoid adverse impacts to falcons and their habitats.

Standards and Guidelines - Peregrine Falcon Habitat

1. For proposed projects within two miles of known falcon nests consider such items as: 1) human activities (aircraft, ground and water transportation, high noise levels, and permanent facilities) which could cause disturbance to nesting pairs and young during the nesting period March 15 to July 31; 2) activities or habitat alterations which could adversely affect prey availability. (G)

2. Within 15 miles of all known nest sites, prohibit all use of herbicides and pesticides which cause egg shell thinning as determined by risk assessment (USDA-Forest Service, September 1992). (S)

3. Restrict climbing and other human disturbances from March 15 through July 31 to avoid adverse impacts at known falcon nest sites. (S).

Objective - Wolverine Habitat

Within two years of the ROD complete a GIS inventory to identify potential wolverine natal den sites. Within 4 years of the ROD, survey all potential wolverine natal den sites to document wolverine presence.

Goal - Goshawk Habitat

Provide suitable habitat conditions for known active and historic goshawk nesting territories.

Standard and Guideline - Goshawk Habitat

Management standards and guidelines for all forest types within active and historic goshawk nesting territories follow:

Attribute	Nest Area	Post-Fledging Family Area	Foraging Area
Number of areas (S)	1	1	1
Size of each area (acres) (S)	>= 200 acres	>= 400	>= 5,400
Size-Class Distribution for forested acres (%): (G)			
nonstocked/seedling	0	<= 20	<= 20
sapling	0	<= 20	<= 20
pole	0	<= 20	<= 20
mature/old growth 1/ <i>2/1000</i>	100	>= 40	>= 40
Rotation age (years) (G)	—	60 to 240	60 to 240
Maximum created opening (acres) (G)	0	<= 40	<= 40
Snags and Reserve Trees 2/ (G)	>= 60% unless specified higher in prescription	>= 60% unless specified higher in prescription	>= 60% unless specified higher in prescription
Downed logs (average/acre) (G)	Forestwide S&Gs	Forestwide S&Gs	Forestwide S&Gs
Management Season (S)	Oct-Feb	Oct-Feb	Year-long
Thinning (G)	Non-uniform 3/	Non-uniform	by silvicultural prescription
Open Road Density 4/ (G)	No new system roads	No new system roads	<= Management Rx Density
1/ Mature and old growth canopy closure for nest sites and post-fledging family areas should range between 75-100 percent. (G) 2/ Refer to previous section on snag/cavity nesting habitat for explanation of biological potential. 3/ Maximize diversity of structure. 4/ Open roads in goshawk territories will be given priority for closure to meet management prescription road density standards. First priority will be to close roads in nest areas; second priority in post-fledging family areas; third priority in foraging areas. Where possible, open road density should be zero in the nest areas and the post-fledging family areas.			

Standard and Guideline - Flammulated Owl Habitat

Do not allow timber or firewood harvest activities within a 30-acre area around all known flammulated owl active and historic nest sites. (S)

Standards and Guidelines - Boreal Owl Habitat

1. Do not allow timber or firewood harvest activities within a 30-acre area around all known boreal owl active and historic nest sites. (S)

2. Maintain over 40 percent of the forested acres in late seral age classes within a 3,600-acre area around all known boreal owl nest sites. (G)

Standards and Guidelines - Great Gray Owl Habitat

1. Do not allow timber or firewood harvest activities within a 20-acre area around all known great gray owl active and historic nest sites. Vegetation manipulation does not include tree planting. (S)
2. Maintain over 40 percent of the forested acres in late seral age classes within a 1,600-acre area around all known great gray owl nest sites. (S)
3. Restrict the use of strychnine poison to control pocket gophers within a 1/2-mile buffer around all known active great gray owl nest sites. (G)

Goals - Trumpeter Swan Habitat

1. Maintain habitat to support ten breeding pairs or more on the Forest.
2. Protect emergent vegetation along shorelines. Maintain riparian vegetation in desired vegetative condition.

Standards and Guidelines - Trumpeter Swan Habitat

1. Maintain suitable trumpeter swan nesting habitat conditions including (but not limited to) the following lakes and ponds: Boundary Pond, Swan Lake, Lily Pond, Hatchery Butte, Railroad Pond, Mesa Marsh, Bear Lake, Upper Goose Lake, Long Meadows, Thompson Hole, Twin Lakes, Chain Lakes, Widgee Lake, Rock Lake, Indian Lake, Putney Meadows, Unnamed Pond (Sec. 19, T9N, R46E). (S)
2. Change livestock grazing through management or fencing when grazing is adversely affecting trumpeter swan use or productivity. (G)
3. No vegetation management will occur within 300 feet of the lake or pond shoreline unless necessary to improve riparian habitat conditions favorable for trumpeter swans. Management may occur after the swans have left the lake or pond. (S)
4. Maintain constant water levels; allow no drawdowns from May 1 to September 30 when not in conflict with preexisting water rights. (G)
5. Do not take any recreation management actions that would encourage dispersed recreation activity at these lakes and ponds. Close these areas to recreation activity if this activity is adversely affecting trumpeter swan use or productivity. (G)
6. Implement habitat improvement projects at these lakes and ponds, such as dredging to maintain proper water depths and aquatic vegetation control. (G)

Goal - Spotted Frog Habitat

Maintain riparian vegetation in desired vegetation condition.

Goals - Common Loon Habitat

1. Evaluate the potential to provide and maintain suitable breeding habitat for common loons at these sites: Indian Lake, Thompson Hole, Bergman Reservoir, Junco lake, Fish Lake, Loon Lake, Moose Lake, unnamed pond (Sec. 9, T47N, R118W).

376-CC

CC-376

12% OG
11.8% Bank

12.1%
Forest
2013!



United States
Department of
Agriculture

Forest
Service

August 2013



Final Environmental Impact Statement

For the Revised Land Management Plan

Idaho Panhandle National Forests

Notes =

10.8%
loss OG
349!!

Part OG
10% PWD
21%

Land Use
Assessment

366-
Ch 5P
12 FL
25 FX

FO
P. NW
OG
10% to log

11%
F. P. NW
NOG
MOOSE

19-OG-no
20 LAD

may be
326

natural snag abn (349)
avg = 10.4 (10-19.9)

Notes =
361

Chapter 3. Affected Environment and Environmental Consequences

In January of 2000 the Forest Service released a Landbird Strategic Plan (USDA Forest Service 2000). The primary purpose of the strategic plan was to provide very general guidance for the agency's landbird conservation program. Among the suggested actions was the incorporation of landbird management into Forest Plans.

A recent report issued by several organizations and federal agencies summarized the general condition of birds across the United States (North American Bird Conservation Initiative 2009, 2011). It painted a picture of declines in multiple species across a variety of habitats. Climate change was one of the contributing factors to these declines, and is likely to continue impacting birds into the future. As the climate warms, breeding seasons and migrations are being altered. These activities may become out of sync with prey abundance, and climate change may also impact where and when those food items are available. This reinforces the need to have resilient habitat that is better able to handle climate change.

The following series of tables (tables 83 through 86) are included to provide a framework to focus the discussion and analysis by focusing on migratory bird priority species and habitats.

Partners in Flight (PIF) produced a North American Landbird Conservation Plan in 2004 (Rich et al. 2004). Their plan was broken down by "biomes" and the Forest is located within the Intermountain West Avifaunal Biome, which includes several Bird Conservation Regions and encompasses several western states. Their plan is very broad in scale. Table 83 displays the species they identified for continental importance within the Intermountain West Avifaunal Biome.

Table 83. Species of Continental Importance Identified for the Intermountain West Avifaunal Biome in the Partners in Flight North American Landbird Conservation Plan (Rich et al. 2004)

Species	Primary Habitat	Is the Forest within the Range of the Species? ¹
Immediate Action²		
Gunnison Sage-Grouse	Western shrublands	N
Greater Sage-Grouse	Western shrublands	N
Bendire's Thrasher	Western shrublands	N
California Condor	Various	N
Spotted Owl	Coniferous Forest	N
Management³		
Brewer's Sparrow	Western shrublands	Y
Pinyon Jay	Woodland	N
Lewis's Woodpecker	Riparian	Y
Cassin's Finch	Coniferous forest	Y
Willow Flycatcher	Riparian	Y
White-throated Swift	Various	Y
Rufous Hummingbird	Western shrublands	Y
Black Swift	Various	Y
Olive-sided Flycatcher	Coniferous forest	Y
Swainson's Hawk	Grassland	Y
Grace's Warbler	Mixed forest	N
Long-term Planning and Responsibility⁴		



United States
Department of
Agriculture

Forest Service

April 2018



Glacier Loon Fuels Reduction and Forest Health Project

Draft Decision Notice

Swan Lake Ranger District, Flathead National Forest
Missoula County, Montana



PA 37,320 - 2
Wild = 12,000 - 28
25,320 = PA Road
39.6 sq mi.

timeline
- 5 yr after log - 30

Timeline 8 yr
5-18

Monitor
0-29

April 2018

OLD GROWTH ASSOCIATED WILDLIFE

INTRODUCTION

Old growth is defined in Amendment 21 of the Forest Plan as "a community of forest vegetation that has reached a late stage of plant succession." The generic description is as follows:

- The age of the dominant cohort of trees is significantly older than the average time interval between natural disturbances (interval will vary depending upon forest cover type and habitat type);
- Forest composition and structure are different from younger stands;
- Rates of change in composition and structure of the stand are slow relative to younger forests;
- There is a significant showing of decadence (wide range of defect and breakage in both live and dead trees).

In The Dictionary of Forestry (Helms 1998), old growth forests are described as having:

- Large trees for the species and site;
- Accumulations of large dead standing and fallen trees;
- Decay or breakage of tree tops, boles, or roots;
- Multiple canopy layers;
- A wide variation in tree size and spacing; and
- Canopy gaps and understory patchiness.

The characteristics of old growth forest described above provide habitat for many plant and animal species. Old growth forests are an important component of biological diversity. For the purpose of this discussion, old growth associated species includes any wildlife species that use the various attributes of old growth forests for some or all of their ecological needs. These needs could include nesting, denning, security, or foraging habitat. For some species, closed canopy old growth provides snow capture and reduces snow depths, insulates the animals from cold winds, and provides protection from predators. Some species, such as the fisher, are strongly tied to canopy cover and mature forest structure for the majority of their habitat needs. More open canopies, or open understories, provide foraging opportunities for prey and predator species alike. Wildlife may use interior old growth habitat as shelter from sun, heat, dryness, or wind and old growth cover may provide protection from predators. Some old growth associated wildlife species need only a portion of their home range to be in old growth; examples include the Canada lynx, northern goshawk, and American marten. Other species such as southern red-backed voles, chestnut-backed chickadee, Swainson's thrush, and northern flying squirrels, have relatively small home range sizes (less than 400 acres), with the necessary proportion of this home range being in old growth unknown.

The following table displays 31 old growth associated species that may be found in the Swan Valley, along with their associations with various old growth habitat characteristics (USDA 1999b).

TABLE 3- 87 HABITAT REQUIREMENTS OF OLD GROWTH ASSOCIATED WILDLIFE SPECIES. (BASED ON WARREN 1998 AND LRMP AMENDMENT 21 FEIS).

SPECIES	COVER TYPE IN AFFECTED AREA	CANOPY	EDGE	LARGER PATCHES	SNAG	DOWN LOG	OCCURRENCE
American Marten	Mixed mesic, lodgepole, spruce/fir forests	Closed	-	+	X	X	Known current
Bald Eagle (S)	Mixed mesic forests, near large lake or river	Open		+	X		Known current
Black-backed Woodpecker (S)	Lower Montane & Montane; post-fire or insect-epidemic forests	Open			X		Known current
Boreal Owl	Mixed mesic and spruce/fir forest mosaic	Closed			X	X	Known current
Brown Creeper	Mixed mesic, lodgepole, and spruce/fir forests	Closed	-		X		Known current
Canada Lynx (T1)	Mixed mesic, lodgepole, and spruce/fir forests; gentle terrain		+2	+	X3	X	Known current
Chestnut-Backed Chickadee	Mixed mesic and spruce/fir forests, especially cedar-hemlock	Closed	-4		X		Known current
Fisher (S5)	Mixed mesic and lodgepole forests	Closed				X	Known current
Flammulated Owl (S, F ⁶)	Lower Montane and Montane, single-story.	Open			X		Known current
Golden-crowned Kinglet	Mixed mesic, lodgepole, and spruce/fir forests	Closed		+	X		Known current
Hairy Woodpecker	Mixed mesic, lodgepole, and spruce/fir forests	Open			X	X	Known current
Hammond's Flycatcher (F)	Mixed mesic and spruce/fir forests	Closed					Known current
Harlequin Duck (S)	Swift mountain streams, riparian old growth (weak association)	Open				X	Known current
Hermit Thrush	Dry mixed mesic and spruce/fir forests	Open		+			Known current
Lewis' Woodpecker	Lower Montane ponderosa pine and old burns	Open			X		Known current
Northern Flying Squirrel	Mixed mesic and lodgepole forests			+	X	X	Known current
Northern Goshawk	Single or multistory old growth; clear forest floor	Closed		+	X		Known current
Pileated Woodpecker	Mixed mesic forests	Closed		+	X	X	Known current
Pine Grosbeak	Mixed mesic, lodgepole, and spruce/fir forests						Known current
Pygmy Nuthatch	Large single-story ponderosa pine and mixed mesic forests	Open			X		Known current
Red-Breasted Nuthatch	Mixed mesic, lodgepole, and spruce/fir; relatively dry	Open		+	X		Known current
Silver-haired Bat	Mixed mesic and lodgepole forests; caves and snags				X		Suspected
Southern Red-backed Vole	Mixed mesic, lodgepole, and spruce-fir forest				X	X	Known current
Swainson's Thrush (F)	Mixed mesic and lodgepole forest with shrub understory			+			Known current
Tailed Frog	Cold, high gradient headwater streams					X	Known current

TABLE 3- 87 HABITAT REQUIREMENTS OF OLD GROWTH ASSOCIATED WILDLIFE SPECIES. (BASED ON WARREN 1998 AND LRMP AMENDMENT 21 FEIS).

SPECIES	COVER TYPE IN AFFECTED AREA	CANOPY	EDGE	LARGER PATCHES	SNAG	DOWN LOG	OCCURRENCE
Three-toed Woodpecker	Mixed mesic, lodgepole, and spruce/fir forests; post-fire				X		Known current
Townsend's Warbler	Mixed mesic and lodgepole forest; dense understory	Closed	-	+			Known current
Varied Thrush	Mixed mesic and spruce/fir forests, especially cedar-hemlock	Closed		+			Known current
Vaux's Swift (F)	Mixed mesic and spruce/fir forests; large hollow snags				X		Known current
White-breasted Nuthatch	Large single-story ponderosa pine	Open			X		Known current
Winter Wren	Mixed mesic and spruce/fir forests, especially cedar-hemlock		-	+	X		Known current
¹ T = Threatened ² + = Positive correlation (where known) ³ X = Important Habitat Component ⁴ - = Negative correlation (where known) ⁵ S = Sensitive ⁶ F = Forest-dwelling Neotropical migrant with apparently declining populations							

ANALYSIS AREA

SPATIAL BOUNDS

The effects analysis area for direct, indirect, and cumulative effects to old growth associated wildlife species is the Glacier Loon Project Area (37,320 acres). This area is large enough to include the home ranges of old growth associated species, and is representative of the effects of fire, natural tree mortality, timber harvest, and road management across the landscape. At the same time, this analysis area is small enough to not obscure the effects of the alternatives. A multi-scale assessment has also been conducted to address habitat diversity concerns.

TEMPORAL BOUNDS

The length of time for effects from the proposed fuels reduction and forest health treatments is approximately 1 to 5 years. This is based on the probable contract length for the proposed project, and the timeframes for related activities.

DATA SOURCES, METHODS, AND ASSUMPTIONS USED

Data used included stand exams, field surveys of snags and down woody logs, old growth surveys, project area field visits, research literature, and GIS and dataset information for features, such as general forest attributes, habitat type, and forest type.

MEASUREMENT INDICATORS

The effects analysis will focus on:

1. Effects to old growth habitat, and
2. Potential effects to old growth associated wildlife species.

April 2018

SNAG AND DOWN WOODY ASSOCIATED SPECIES

INTRODUCTION

Snags, broken-topped live trees, down logs, and other woody material are required by a wide variety of species for nesting, denning, roosting, perching, feeding, and cover (Bull et al. 1997). Snags and down, dead, material are also used for communication purposes:

- Singing, (songbirds),
- Drumming (grouse and woodpeckers),
- Calling (squirrels, jays, birds of prey), and
- Sight recognition posts.

Small mammals and birds use standing and down dead material for food storage and for hunting. Down logs and stumps are important for travel, both below the snow in the winter, and as travel cover throughout the year. It is estimated that about one third of the bird and one third of the mammal species that live in the forests of the Rocky Mountains use snags for nesting or denning, foraging, roosting, cover, communication, or perching. On the Flathead National Forest, at least 42 species of birds and 10 species of mammals are dependent on dead wood habitat for nesting, feeding, or shelter (USDA 1999b). The more mobile species that depend on dead wood habitat include black bears, Canada lynx, wolverines, marten, fisher, bats, woodpeckers, and small owls. Less mobile species that depend on dead wood include snowshoe hares (the primary prey of Canada lynx), red-backed voles (the primary prey of marten, fisher, boreal owl, and several other species), shrews, bryophytes, lichen, fungi, and protozoa. As down woody material further decays, it plays an important role in nutrient cycling, soil fertility, and erosion control.

Snags and their management have become a major conservation issue in managed forests across the western United States. Biologists have recognized for a long time that snags and down woody material provide important wildlife habitat, but only in the last decade or so have managers begun to understand that not only is tree decay an important ecological process that affects wildlife habitat (Bull et al. 1997), but snags and dead wood are an essential, important part of the larger ecosystem. The number, species, size, and distribution of available snags strongly affect snag-dependent wildlife. An insufficient number of suitable snags may limit or eliminate populations of cavity-using species (Saab et al. 1998; Thomas et al. 1979).

Although various sizes of snags and down woody are used, larger birds and mammals require larger dead trees. The larger-diameter down trees provide stable and lasting structure and offer better protection from weather extremes (Bull 2002). Longer down woody pieces provide better runways, shelter, and under-snow access.

Several wildlife species that use snag and down woody habitats on the Flathead National Forest are USFS Region One Sensitive Species, including the bald eagle, black-backed woodpecker, fisher, flammulated owl, Townsend's big-eared bat, and wolverine. One of the TES Species on the Flathead National Forest, the Canada lynx, has a strong habitat association with down woody material (denning).

Snags are essential habitat for at least 42 species of birds and 10 species of mammals in Montana. Table 3- 88 displays specific habitat relationships and Montana NHP rankings for wildlife species in Montana associated with snag, "defective" live tree, or down woody habitat.

GLACIER LOON FUELS REDUCTION AND FOREST HEALTH PROJECT

CHAPTER 3

WILDLIFE - SNAG AND DOWN WOODY ASSOCIATED SPECIES

TABLE 3- 89 SPECIES THAT USE SNAGS, "DEFECTIVE" LIVE TREES, AND/OR DOWNED LOGS.

SPECIES	GLOBAL & STATE RANKS (MTNHP 2009) "	SNAG DBH (INCHES)	SNAG HEIGHT (FEET)	DOWNED LOGS?	OCCURRENCE
American Kestrel (N)	G5, S5B	17	20		Known current
Bald Eagle (S)	G5, S3, SOC	25	40		Known current
Barred Owl (former MIS)	G5, S4	25	30		Known current
Barrow's Goldeneye	G5, S4, potential SOC	25	10		Known current
Big Brown Bat	G5, S4	17	20		Known current
Black-backed Woodpecker (S)	G5,S3 (SOC)	17	10		Known current
Black-capped Chickadee	G5, S5	9	10		Known current
Bobcat	G5, S5	-	-	yes	Known current
Boreal Chickadee	G5,S3 (SOC)	9	10		Known current
Boreal Owl (former S)	G5, S4	17	10		Known current
Brown Creeper	G6, S3, SOC	15	20		Known current
Bufflehead	G5, S5B	17	10		Known current
Canada lynx (T)	G5, S3, SOC	-	-	yes	Known current
Chestnut-backed Chickadee	G5, S4	9	10		Known current
Common Goldeneye	G5, S5	25	10		Known current
Common Merganser	G5, S5B	17	10		Known current
Dark-eyed junco	G5, S5B	-	-	yes	Known current
Downy Woodpecker	G5, S5	11	10		Known current
Fisher (S)	G5, S3, SOC	25	30	yes	Known current
Flammulated Owl (S, N)	G4, S3B, SOC	17	10		Known current
Great Horned Owl	G5, S5	25	30		Known current
Hairy Woodpecker	G5, S5	17	20		Known current
Harlequin Duck (S)	G4, S2B, SOC	-	-	yes	Known current
Hooded Merganser	G5, S4, potential SOC	17	10		Known current
House Finch	G5, S5	15	10		Known current
House Sparrow	G5, undesired species	15	20		Known current
House Wren (N)	G5, S5B	15	10		Known current
Lewis' Woodpecker	G4, S2B (SOC)	17	30		Known current
Little Brown Myotis	G5, S4	17	10		Known current
Long-eared Myotis	G5, S4	17	10		Known current
Long-legged Myotis	G5, S4	17	10		Known current
Long-tailed Weasel	G5, S5	-	-	yes	Known current
Marten (former MIS)	G5, S4	17	20	yes	Known current
Mountain Bluebird	G5, S5B	15	10		Known current
Mountain Chickadee	G5, S5	9	10	yes	Known current
Northern Alligator Lizard	G5,S3 (SOC)	-	-	yes	Known current
Northern Flicker	G5, S5	17	10		Known current
Northern Flying Squirrel	G5, S4	17	20		Known current
Northern Goshawk (former S)	G5,S3 (SOC)	-	-	yes	Known current
Northern Hawk Owl	G5, S4, potential SOC	25	10		Known current
Northern River Otter	G5, S4	-	-	yes	Known current
Northern Waterthrush (N)	G5, S5B	-	-	yes	Known current
Osprey	G5, S5B	17	40		Known current

TABLE 3- 89 SPECIES THAT USE SNAGS, "DEFECTIVE" LIVE TREES, AND/OR DOWNED LOGS.

SPECIES	GLOBAL & STATE RANKS (MTNHP 2009) "	SNAG DBH (INCHES)	SNAG HEIGHT (FEET)	DOWNED LOGS?	OCCURRENCE
Painted Turtle	G5, S4	-	-	yes	Known current
Pileated Woodpecker (former MIS)	G5,S3 (SOC)	25	60		Known current
Pygmy Nuthatch	G5, S4	17	30		Known current
Pygmy Owl	G5, S4	17	30		Known current
Raccoon	G5, S5	25	10		Known current
Red-breasted Nuthatch	G5, S5	17	20		Known current
Red-naped Sapsucker (N)	G5, S4B	17	20		Known current
Rubber Boa	G5, S4	-	-	yes	Known current
Ruffed Grouse	G5, S4	-	-	yes	Known current
Saw-whet Owl	G5, S4	17	20		Known current
Silver-haired Bat	G5, S4, potential SOC	17	20		Known current
Southern Red-backed Vole	G5, S4	-	-	yes	Known current
Spruce Grouse	G5, S4	-	-	yes	Known current
Striped Skunk	G5, S5	-	-	yes	Known current
Swainson's Thrush (N)	G5, S5B	-	-	yes	Known current
Tailed Frog	G5, S4	-	-	yes	Known current
Three-toed Woodpecker	G5, S4	17	20		Known current
Tree Swallow (N)	G5, S5B	15	20		Known current
Vaux's Swift (N)	G5, S4B	25	40		Known current
Violet-Green Swallow	G5, S5B	15	20		Known current
Western Bluebird	G5, S4B	15	10		Known current
Western Jumping Mouse	G5, S4	-	-	yes	Known current
Western Screech Owl	G5, S3, potential SOC	17	20		Known current
Western (Townsend's) Big-eared Bat (S)	G4, S2 (SOC)	?	?		Known current
White-breasted Nuthatch	G5, S4	17	20		Known current
Williamson's Sapsucker (N)	G5, S4B	17	20		Known current
Wilson's Warbler (N)	G5, S5B	-	-	yes	Known current
Wolverine (S)	G4, S3 (SOC)	-	-	yes	Known current
Wood Duck	G5, S5B	25	10		Known current
Yuma Myotis	G5, S3, potential SOC	17	10		Known current

T=Threatened; S=Sensitive Species; N=Neotropical migratory bird; Natural Heritage Program Rank: G=species range-wide (global); S=state wide; 2=At risk because of very limited and/or declining numbers, range, and/or habitat, making it vulnerable to global extinction or extirpation in the state. 3=Potentially at risk because of limited and/or declining numbers, range, and/or habitat, even though it may be abundant in some areas. 4=Uncommon but not rare (although it may be rare in parts of its range), and usually widespread. Apparently not vulnerable in most of its range, but possibly cause for long-term concern. 5=Common, widespread, and abundant (although it may be rare in parts of its range). Not vulnerable in most of its range. B=State rank modifier indicating breeding for a migratory species. SOC=Montana Species of Concern.

48 birds

ANALYSIS AREA

SPATIAL BOUNDS

The Glacier Loon Project Area was considered for the evaluation of direct and indirect effects on snag and down woody associated species. This approximately 37,320-acre area is large enough to include the home ranges of several individuals or pairs of a species, and is representative of the effects of fire, natural tree mortality, timber harvest, and road management across the landscape. The actions proposed in the alternatives that could directly or indirectly affect snag or down woody associated wildlife species are contained within this area. The Upper Swan Valley was considered in the cumulative effects analysis. A multi-scale assessment was also conducted to address habitat diversity concerns for dead tree dependent species (USDA 2006).

TEMPORAL BOUNDS

The length of time for effects from the proposed fuels and forest health treatments is approximately 1 to 5 years. This is based on the probable contract length for the proposed project, and the timeframes for related activities.

DATA SOURCES, METHODS, AND ASSUMPTIONS USED

Data used included project area field visits, research literature, and GIS and dataset information for features, such as general forest attributes, habitat type, and forest type.

MEASUREMENT INDICATORS

The effects analysis will focus on:

1. Effects to snag and down woody habitat, and
2. Potential effects to snag/down woody associated wildlife species.

AFFECTED ENVIRONMENT

HISTORICAL CONDITION

Forest ecosystems in the western United States have adapted in response to disturbances such as wildfire, insects, disease, and windstorms. Snags and down woody material have always occurred on the landscape, a direct result of these disturbance factors, either on a large scale, or on a very small scale, as individual trees grow old and die. Ritter and others have described snag populations as occurring in either "pulses" of snags following a large disturbance event, or as "continuous" populations of scattered individuals (Ritter et al. 2000).

Historically, in the Swan Valley, snag habitat and down woody material, though always present in varying amounts, experienced greater "pulses" across the landscape and in localized areas as a result of natural disturbances. Warmer and drier areas historically underwent more frequent, lower-intensity fires, and typically supported fewer snags and large down logs than cooler and moister environments, where the stands reached climax conditions before experiencing stand-replacing fire.

EXISTING CONDITION

The Northern Region of the Forest Service estimated snag densities for Western Montana Forests by



Forest Health Evaluation of the Katkee Fuels Project Area
Bonniers Ferry Ranger District, Idaho Panhandle National Forests
Coeur d'Alene Field Office Trip Report
CFO-TR-23-013

2024

15,000

Forest Health Protection (FHP) Personnel Present: Sean Wright, Plant Pathologist, sean.wright@usda.gov, 208-446-4508; Danielle Malesky, Entomologist, danielle.malesky@usda.gov, 208-449-6530

Local Contacts: AJ Helgenberg, Zone Silviculturist, Sandpoint Ranger District, Idaho Panhandle National Forests, 208-265-6643; Kyla Berendzen, Silviculturist Forester, Sandpoint Ranger District, Idaho Panhandle National Forests, 208-290-6974; KaliRose Zurfluh, District Fuels Specialist, Sandpoint Ranger District, Idaho Panhandle National Forests, 208-290-6974

Agency/Unit: USDA Forest Service, Idaho Panhandle National Forests, Sandpoint Ranger District

Trip Date: September 18 and November 9, 2023

Keywords: root disease, Armillaria, laminated root disease, western larch dwarf mistletoe, Indian paint fungus, Schweinitzii, yellow root rot, Douglas-fir beetle, wood borers, flat headed fir borer, fir engraver, abiotic stressors

Citation: Wright, S. & D. Malesky. (2023). Forest Health Evaluation of the Katkee Fuels Project Area. FHP Trip Report CFO-TR-23-13. Coeur d'Alene, ID: U.S. Dept. of Agriculture, Forest Service, Northern Region, Forest Health Protection. 34p.

Location: The Katkee Fuels Project Area lies 8 miles east and southeast of Bonners Ferry, ID, in an area between the Kootenai River on the northeast and Black Mountain on the southwest.

Size (acres): Project area approximately 15,000 acres with treatment units on approximately 9,150 acres

61%

Primary Forest/Cover Type(s) by decreasing prevalence: western larch, lodgepole pine, grand fir, Douglas-fir, western redcedar, western hemlock, ponderosa pine, western white pine

Project Objectives: The project is designed to mitigate hazardous fuels and improve public safety by restoring a more diverse and resilient forest structure within the wildland urban interface.

Primary Damage Agents Observed - Tree Species Affected:

1) Root disease complex:

- a. Armillaria root disease (*Armillaria ostoyae*) - Douglas-fir, grand fir, lodgepole pine, western white pine, western redcedar, western hemlock
- b. Heterobasidion Root Disease (*Heterobasidion occidentale*) - western hemlock, Douglas-fir

- c. Schweinitzii root and butt rot (*Phaeolus schweinitzii*) – Douglas-fir
- d. Cedar laminated root and butt rot (*Phellinus weirii*) – western redcedar
- e. Yellow root rot – (*Poriella subacida*) –ponderosa pine, lodgepole pine
- 2) Larch dwarf mistletoe (*Arceuthobium laricis*) – western larch
- 3) Larch needle blight (*Hypodermella laricis*) – western larch
- 4) Larch needle cast (*Meria laricis*) – western larch
- 5) Red ring rot (*Porodadalea pini*) – western larch, lodgepole pine
- 6) Indian paint fungus (*Echinodontium tinctorium*) – western hemlock
- 7) Cedar brown pocket rot (*Oligoporus sericeomollis*) – western redcedar
- 8) Pouch fungus (*Cryptoporus volvatus*) – Douglas-fir
- 9) White pine blister rust (*Cronartium ribicola*) – western white pine
- 10) Western gall rust (*Endocronartium harknessii*) – lodgepole pine
- 11) Bark beetles and woodboring insects:
 - a. Fir engraver (*Scolytus ventralis*) – grand fir
 - b. Ambrosia beetles (Scolytinae and/or Platypodinae) – grand fir
 - c. Douglas-fir secondary insects (*Scolytus monitcolae*) – Douglas-fir
 - d. Western pine beetle (*Dendroctonus brevicornis*) – ponderosa pine
 - e. Pine engraver beetle (*Ips pini*) – ponderosa pine
 - f. Woodborers (Cerambycidae and Buprestidae) – across all observed recently dead and dying conifers
- 12) Defoliators:
 - a. Douglas-fir needle midge (*Contarinia* spp.) – Douglas-fir
 - b. Larch looper (*Macaria sexmaculata*) – western larch
 - c. Larch casebearer (*Coleophora laricella*) – western larch
- 13) Sucking insects:
 - a. Pine needle scale (*Chionaspis pinifoliae*) – lodgepole pine
 - b. Pine aphids (*Pineus* spp.) – lodgepole pine

Observations of Important Forest Diseases and Insects:

The most common and destructive forest diseases and insects we observed were root diseases, stem decays, dwarf mistletoe, bark beetles, and aphids and scales. Root diseases were present in all units. Bark beetles, past bark beetle activity, and woodborers were confirmed in all units. The units with small diameter regeneration size class pine and larch had higher amounts of defoliator activity and sucking insect-caused tree damage. For a table of detailed disease, insect, host, and stand conditions refer to the Appendix A, Table 1.



Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Rocky Mountain Region, Shoshone National Forest

March 2024

Green Union Project

Draft Environmental Assessment



bank from site access and operations would be very similar to vegetation removal. These effects would be limited to areas where disturbance is at higher intensity levels, such as temporary roads and landings. Effects to the seed bank would be minimized through the application of standard soil design features incorporated to minimize detrimental soil conditions that persist over the long-term, such as rehabilitation components and operating condition restrictions.

Prescribed burning (broadcast burning, jackpot burning, and pile burning) may result in mortality to trees and damage seed viability in seedbanks through soil heating. Burn timing and conditions, as well as project design should minimize these effects. Rehabilitation of pile burn areas (soil ripping, seeding, and planting) may create larger openings in the canopy and foster seedling establishment and caching sites.

Tree seedling planting would occur in the project areas as needed. Some units will be planted with whitebark pine seedlings where conditions are likely to support long-term survival and stand development. Seeds will be sourced from the appropriate white pine blister rust resistant genetic stock. Rust resistant seedlings will promote healthier stands and may be more resilient in the face of predicted climate change.

Over the long-term, proposed silvicultural and burning treatments would improve forest health, reduce fuel loads, and create fuelbreaks. Prescriptions for specific unit goals (desired tree spacing, composition, insect and disease prevalence, fuel loads, and whitebark pine restoration potential) dictate levels of overstory and understory removal for all species. Whitebark pine would continue to be present in all units where it currently exists. Silvicultural treatments would be designed to retain growing space for whitebark pine under all treatment types at varying levels. Mature, healthy, whitebark pine trees with the highest reproductive potential would be prioritized for retention in concert with treatment goals. Treatments around these trees would maximize full and open crown development that would result in increased tree ring growth, cone production, and reproductive capacity (Keane et al. 2007). Loss of individuals would be focused on suppressed seedlings and saplings, as well as those mature trees that are diseased, damaged, or otherwise have low reproductive capacity (table 6). Table 6 includes loss of individuals both in areas where whitebark pine is a minor part of the forested stands as well as areas where it is a more significant component of stands.

Table 5. Analysis area and acres of whitebark pine habitat affected by treatments in the analysis area. The analysis area is comprised of the entirety of the six watersheds where treatments would occur.

Analysis Area (acres)	Treatment Units (acres)	Percent of Analysis Area Being Treated	Whitebark Pine Habitat in Analysis Area (acres)	Treatment Units in Whitebark Pine Habitat (acres)	Percent of Whitebark Pine Habitat in Analysis Area Affected by Treatments
105,816	9,677	9.1	43,931	2,749	6.5

Table 6. Total number of trees and estimated loss of the number of existing whitebark pine and percent of total loss by size class as a result of project activities

Whitebark Pine Size Class	Estimates of Existing Trees in All Treatment Areas	Mortality from Temporary Roads and Landing Construction	Intentional Mortality (Tree Removal to Address Management Objectives)	Unintentional Mortality (Inadvertent Mortality as a Result of Project Activities)	Total Estimated Mortality
Seedlings	2,481,176 (74%)	92,168 (3.8%)	863,434 (36.2%)	355,480 (14.9%)	1,310,082 (54.9%)

Whitebark Pine Size Class	Estimates of Existing Trees in All Treatment Areas	Mortality from Temporary Roads and Landing Construction	Intentional Mortality (Tree Removal to Address Management Objectives)	Unintentional Mortality (Inadvertent Mortality as a Result of Project Activities)	Total Estimated Mortality
Saplings	756,793 (22.6%)	25,539 (3.5%)	230,914 (31.6%)	95,439 (13.1%)	351,892 (48.1%)
Mature trees	113,998 (3.4%)	3,518 (3.2%)	8,925 (8.1%)	0 (0.0%)	12,433 (11.3%)

Typically, effects to trees would vary from survivable damage to mortality. For this analysis, effects are all considered mortality due to the inability to estimate with any accuracy what damage rates or subsequent survival rates could be across age classes. As a result, estimated mortality is likely higher than what actual mortality may look like after project completion (table 7). Mortality estimates were developed by a forester and silviculturist and were based on literature reference and professional judgment from prior mechanical treatments on the forest. Mortality estimates were calculated based on specific prescriptions and anticipated effects. Some suitable units would be replanted with whitebark pine seedlings after treatment. Temporary roads and landings would be rehabilitated after project activities are completed through soil ripping, seeding, and planting, if required. Once rehabilitated, these areas would provide larger openings in the canopy available for seedling establishment and caching sites.

Cumulative Effects

Vegetation treatments, grazing, recreation, and invasive plant management in conjunction with the proposed action could result in cumulative effects to whitebark pine. Project design features for this and other projects are incorporated to minimize effects.

For whitebark pine, past and ongoing vegetation treatments for fuel reduction, insect and disease management, salvage, and timber management have been authorized in the last 20 years in seven separate projects across the analysis area. Activities associated with vegetation management include planting, temporary road construction, prescribed fire, and mechanical vegetation removal. The effects of these activities are the same as described above for the proposed action. Approximately 11,154 acres have been authorized for treatment in the analysis area that fall within modeled whitebark pine habitat. When combined with the proposed action, 13,903 acres of whitebark pine habitat would be authorized for treatment out of 43,931 total acres of whitebark pine habitat in the analysis area, which amounts to 31.6 percent.

The authorization to treat in whitebark pine habitat does not equate to complete whitebark pine removal. As with the proposed action, treatments in other projects will affect individual trees, but are concentrated in the seedling and sapling size class. Areas where whitebark pine has existed within these project areas continue to support whitebark pine after treatment. These treatments also include beneficial effects to whitebark pine, such as planting, as well as removal of standing dead and infected trees. Treatments in other projects avoid mature whitebark pine removal, using similar methods to the proposed action. Healthy, mature, cone-producing individuals are preferentially retained where possible. Future vegetation treatments have not been identified in the analysis outside those that are ongoing and have already been authorized.

Authorized cattle grazing does not meaningfully interact with whitebark pine habitat. While cattle grazing may affect individuals through hoof action and above ground disturbance in some areas, it would be insignificant and likely undetectable.

States?
31.6%
treat
removal
genetic
diversity



**Montana Fish,
Wildlife & Parks**



**September 27,
2013**



**U.S. Forest Service and Montana Department
of Fish Wildlife and Parks Collaborative Overview and Recommendations for
Elk Habitat Management
on the Custer, Gallatin, Helena,
and Lewis and Clark National Forests**

Abstract:

A group of wildlife biologists from the Forest Service (FS) and Montana Department Fish, Wildlife, and Parks (MDFWP) have compiled recommendations, along with a discussion of their conversations and the relevant literature, for elk habitat management. These are recommendations only, and the group is not making decisions or setting policy for either agency in this effort. While we focus on elk habitat considerations in this effort, we do not advocate for single species management. We advocate for ecologically appropriate habitat management under an umbrella of landscape scale ecosystem management, which focuses on providing a range of habitats to support all fauna native to the landscape, including elk. These recommendations apply only on the Custer, Helena, Lewis and Clark, and Gallatin National Forests.

The recommendations are based on the most current available information and the collective experiences of these biologists. They considered contemporary issues and circumstances such as increases in recreation of all types on these National Forests, changes in the numbers and distribution of elk (including the use of private lands where hunting is limited or not allowed), the restoration of large predators, the current mountain pine beetle epidemic, and small and large fires on the Custer, Helena, Lewis and Clark, and Gallatin National Forests in the Northern Region of the Forest Service. The shared goal of the two agencies is to provide for elk and other big game on National Forest System (NFS) lands throughout the year, recognizing that overall agency missions differ. That is, within the multiple use mandate of the Forest Service, management for elk will be one of many considerations on NFS lands. The overview and recommendations address an appropriate elk analysis unit, management of cover and recreation on winter ranges, security during the archery and rifle hunting seasons, motorized route management relative to habitat effectiveness, cover on spring-summer-fall ranges, cover patch size, forage, calving areas, and migration corridors. The recommendations conclude with a short discussion of considerations for bighorn sheep.

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INTRODUCTION

MDFWP elk population management focuses on maintaining numbers well above population viability thresholds, protecting certain sex and age classes from over-harvest, providing public hunting opportunity, and attempting to balance elk distribution across public and private lands. The FS strives to complement MDFWP's efforts through management of elk habitat on FS lands.

The two agencies share the goals of harvest, population, and other elk and habitat objectives being met (e.g. State Elk Plan, Forest Plan), as well as elk using FS lands in an acceptable way that is proportional to their availability. These goals are the topic of annual coordination meetings between the two agencies. If harvest, population or other elk objectives are not being met, then the two agencies should work together beyond meeting annually in order to identify whether any limiting factor relates to FS habitat management, MDFWP regulations, other factors (e.g., predation, winter kill, disease, climate change, stochastic events, inherent habitat differences between FS lands and other ownerships), or a combination of these.

Forest Plans, which provide overall management direction related to elk habitat, were developed for the Custer, Gallatin, Helena, and Lewis and Clark National Forests between 1982 and 1986. Three of the four forests (Helena, Lewis and Clark, Gallatin) have Forest Plan standards related to the management of roads and forested cover. The Custer National Forest does not have a specific, quantifiable elk standard in its Forest Plan.

Substantial changes have occurred between the 1980's and the present relative to elk numbers, elk distribution, habitat, and hunting season structures. There has also been on-going elk research efforts and published literature on the subject of elk habitat management that is important to consider. This overview and the recommendations reflect the efforts of wildlife biologists from the FS and MDFWP to use the best contemporary information and their collective experiences in managing elk and elk habitat to address current issues and conditions on the four National Forests.

ACKNOWLEDGEMENTS

This effort took place over a nearly three year time period and involved a series of meetings and conference phone calls involving wildlife biologists from the FS and the MDFWP. While participation by individuals at meetings varied, there was a core group from both agencies that conducted literature reviews, and document writing and editing. This group also interfaced with academic elk experts and researchers (see list of editors, reviewers, and contributors at the conclusion of the paper), as well as corresponding managers, planners, and line officers. The contributions of all those who attended meetings and who completed assignments to provide information and/or analysis to help further the discussions were tremendous. While the effort incorporated scientific research, literature, and survey information, many of the recommendations were influenced by our collective years and experience with managing elk populations and elk habitat and were the product of our thoroughly discussed, professional judgments. We hope that this effort stimulates constructive criticism and new research that, along with a continuing evaluation of the utility and content of these recommendations, would be used in promoting adaptive changes in the management of elk and elk habitat. To keep up with

current science on elk and habitat management, this document is intended to be updated periodically through continued partnership between the FS and MDFWP.

A significant aspect of this effort is the recognition of the importance of on-going collaboration between the two agencies regarding the management of elk populations and habitat. As used here, collaboration refers to at least one annual meeting between the FS (Forest level) and MDFWP (Regional level). For the FS this will include a line officer representative and the Forest Biologist. **Appendix A** includes some decision diagrams intended to facilitate collaboration between the two agencies and to identify limiting factors that would inform elk herd specific strategies.

We also recognize the importance of frequent dialogue between personnel from the two agencies at the local level. This interchange needs to be proactive and occur before, during, and after specific management actions are proposed, implemented, and monitored.

INTENDED GEOGRAPHIC AREA

The area of applicability includes all of the four National Forests mentioned above within the state of Montana. There is a portion of the Custer National Forest within South Dakota. While elk occur on the South Dakota portion of the Sioux District, there currently is no hunting season, so recommendations that revolve around hunting would not apply there. Non-hunting recommendations could be considered in conjunction with the South Dakota Department of Game, Fish, and Parks biologist for that area.

This area ranges from just west of the continental divide on a portion of the Helena National Forest to the southern and eastern borders of the state and encompasses the island mountain ranges of central Montana. The area includes both sizeable continuous blocks of National Forest lands as well as scattered smaller blocks. Habitats include alpine coniferous forests, shrublands, grasslands, and riparian areas. Coniferous forests on these four National Forests tend to be more open and dry than coniferous forests west of the Continental Divide. Disturbances such as fire and insect-caused mortality of trees are major influences on the vegetation dynamics of this geographic area. In addition, these National Forests are interspersed with large areas of private land.

The proportion of FS lands in a Hunting District (HD) or Elk Management Units (EMU) varies greatly. As the amount of FS lands varies substantially within the geographic units that MDFWP uses as a basis for setting population objectives and other metrics, it is sometimes difficult to make inferences about elk numbers, distribution, and/or seasonal use of habitat within the administrative boundaries of NFS lands. Trending from west to east, NFS lands are a smaller portion of the land ownership matrix, and often receive hunting pressure and general recreational use disproportionate to their occurrence on the landscape, which may contribute to the displacement of elk from public to private lands.

OBJECTIVES

The objective of this document is to capture the extensive discussion and collaboration that took place between wildlife biologists and managers (FS), and area biologists and managers (MDFWP) on

matters related to elk and other big game, and the habitat needs for maintaining these species on public lands represented by these four national forests.

The shared goal of the biologists involved in this effort is to maintain and provide for big game wildlife species on NFS land throughout the year. The agencies also recognize the differences in their missions and that the management of big game does not always take precedence in the management of NFS lands. However, it was agreed that some considerations for big game habitat are valid both programmatically (Forest Plans) and at the project level to help achieve this mutual goal.

The recommendations are intended to also serve the public's strong interest in big game management and enjoyment of wildlife (a publicly owned resource) on public land for the purposes of hunting, wildlife viewing, and for other values and ecological roles (e.g. herbivory, predator prey dynamics, a source of carrion, etc.) of wild ungulates. Although the objective applies broadly to most big game species, the content of the recommendations refers specifically to elk. It was recognized, that in some cases, big game species other than elk will be as, or more important to consider relative to site-specific project level impacts.

These recommendations and the discussions around which the agency participants arrived at consensus provide a foundation to account for current understanding of issues, management emphases, and the body of knowledge represented in the literature relative to elk and habitat management. The agency participants recognize that their recommendations do not address all types of management actions (e.g. energy development).

CURRENT ISSUES RELATED TO ELK MANAGEMENT

Elk numbers have been increasing across the west and in Montana since the early to mid-1900s. Statewide, post-season elk numbers increased from 8,000 in 1922 to 55,000 in 1978 and to about 141,000 in 2011. As such, there are no viability concerns for Rocky Mountain elk in Montana or on any of the four Forests. This is supported by their global status of "G5" and the statewide status of "S5" which are both defined as "common, widespread, and abundant..." However, elk remain a management indicator species, as well as an economically and socially important species with large public interest. They continue to provide hunting, wildlife viewing, and photography opportunities, and to fill ecological roles associated with having this native species on the landscape.

Elk inhabit much of the area covered by these four Forests. Elk populations are dynamic, but have generally expanded and increased in numbers since the Forest Plans were adopted in the late 1980's. Some elk populations are above State Elk Plan objectives for the respective Elk Management Unit (MDFWP 2005). Populations above the State Elk Plan objective represent non-compliance with the management plan and should not be generally interpreted as a positive condition based on state law.

Currently, in some areas of Montana, the distribution of elk has become a primary management issue. In some areas elk are present and spending significant amounts of time on private lands. Issues with displacement from public lands to private lands, or disproportionate use of private lands are

widely recognized, and there are multiple contributing factors. These factors potentially include differences in access for hunting, habitat condition, hunting regulations, and other factors such as predation, climate change, stochastic events, inherent habitat differences between FS lands and other ownerships, or a combination of these.

MDFWP generally uses Hunting District and Elk Management Unit boundaries to gather information on population objectives, hunting success, bull-cow ratios, and other aspects of elk management. The proportion of a hunting district or elk management unit that is in part comprised of FS lands varies greatly. The FS does not monitor elk or other big game and relies on MDFWP for information on elk population trends. Since the surveys conducted by MDFWP do not occur exclusively on FS lands, it is difficult to draw inferences on elk population effects from habitat management on FS lands.

The lack of public access to hunt big game on private lands and the resulting differences in relative hunting pressure can play a major role in elk population dynamics and distribution. Human disturbance and potential for displacement of big game animals is not restricted to the 5- week rifle season currently in place in Montana. Because archery hunting has increased significantly in popularity, there has been a noted shift in some cases of elk moving to private land, as a result of displacement during the archery season. Human disturbance may also influence elk habitat use and distribution during time periods outside of the hunting season. In addition, predators (generally mountain lions, wolves, and bears) also influence elk population dynamics and distribution in some areas.

Cover dynamics also have the potential to affect elk habitat use (Peek et al. 1982, Unsworth et al. 1988). However, our management paradigm regarding the relationship between cover and elk reflected by the work Lyon et al. completed in 1985 (elk and timber management) was based on a focused road building and timber management program on Montana forests. That paradigm currently has shifted towards smaller, more focused fuel reduction thinning projects; although, the pendulum could swing back toward larger timber harvest projects in the future. Many forested areas that were regenerated by timber harvest (from the 50's, 60's, and 70's) have largely recovered and are healthy sapling and pole sized forested stands. However, insects and diseases have reduced the amount of mature live coniferous tree cover that is available on the landscape. These impacts are currently most notable on the Helena National Forest, but have also affected the amount of live coniferous cover on the other National Forests that are included in this assessment. Small and large fires have also affected cover availability.

Forage remains a key habitat attribute affecting elk population dynamics and distribution, as well as their use of a landscape. Forage quality and quantity can be affected by domestic grazing, noxious weeds, fire, and forest management.

OVERVIEW AND RECOMMENDATIONS

1. Scale and Scope of an Elk Habitat Analysis

The recommendation is to use an elk analysis unit (EAU), which in many cases may reflect elk herd unit home ranges as defined by Edge et al. (1986). Edge et al. showed that cow elk segregated into discrete herds and showed fidelity to a specific geographic area. They concluded that this is the normal social structure for the species, and that the herd unit represents the best evaluation area for assessing the impact of various management activities on elk habitat. Ideally, herd unit home ranges are *defined by animals*, typically on the basis of radio relocation data collected over enough time and for all seasons that the annual use patterns of elk form a pattern (Hillis et al. 1991; Lyon and Christensen 1992). Since this level of understanding of herd ranges is not consistently available across the geographic area represented by the four forests, the EAU (*defined by people*) represents the best approximation of a herd unit home range based on local knowledge of biologists from both agencies (as well as other knowledgeable sources). The use of elk analysis units is also consistent with Hillis et al. (1991) and Lyon and Christensen (1992) as they refer to the term “habitat analysis unit” in their work. If there is no observational or survey data on which to delineate the EAU(s) for a given project area, the EAU(s) should be based the best professional judgment of both FS and MDFWP local biologists.

The EAU serves as the unit for examining direct, indirect, and cumulative effects at the project level.

Discussion:

Both agencies agreed that the area for assessing direct, indirect, and cumulative effects to elk habitat is to be identified up front and be biologically defensible.

The state of Montana in its 2005 Elk Plan defines elk objectives by Elk Management Units (EMU). Each EMU encompasses one or more hunting districts that share similar ecological characteristics and, in most cases, encompasses the yearlong range of major elk populations inhabiting the EMU. Hunting districts are somewhat convenient to use in discussions regarding elk populations since those are the basis for setting harvest quotas and hunting regulations. However, FS and MDFWP wildlife biologists agreed that EMUs and hunting districts are too large to appropriately quantify FS project level effects.

Edge et al. (1986) recommended using elk herd unit home ranges as the basic land unit for elk management. Hillis et al. (1991) recommended using the local herd home range during hunting season as the ideal basis for analyzing elk security areas. For the elk herds discussed in Hillis et al., herd units had been determined using telemetry studies (relocations of elk with radio-collars over time). However, Hillis et al. also discussed the use of a standardized “habitat analysis unit” and that in the absence of telemetry defined area, to use the experience of reliable local biologists, hunters, and outfitters.

There was some concern from MDFWP wildlife biologists about drawing elk analysis units without the benefit of telemetry studies. Knowing that this data was not consistently available or likely to become available, the agency participants discussed the use of watersheds (6th code or possible 5th code) as one basis on which to analyze the quality of elk habitat. Watersheds are logical units for many ecological processes and are consistent with Lyon and Christensen (1992) from the perspective of representing a “geographic” boundary. Watershed boundaries also have some biological meaning

relative to elk. For example, Lyon et al. (1985) point out that some topographic features (such as ridgelines) provided line-of-sight barriers between elk and human disturbance, which reduced the displacement distance. The agency participants agreed that a collaborative mapping effort from both agencies' biologists would be needed and based on the best professional judgment of the individuals involved.

The agency participants recognized that there is year to year variability of the areas used by an elk herd, as well as potential overlap of elk herd unit home ranges, either on summer range or on winter range. However, there was an acknowledged need for an analysis tool which provides non-overlapping (to the extent possible), relatively static EAU's to which Forest Plan direction and analyses would be applied. We expect that elk analysis units will be large enough to encompass this natural variation in the way elk use landscapes. EAUs will need to be reviewed periodically (by local FS and MDFWP biologists) to reflect new or better information if and when it becomes available. We recommend that EAU's be re-evaluated at least every 10 years (based on Van Dyke et al. 1998).

Where EAU's include private land, there was some discussion of whether the FS should not only take the habitat conditions and circumstances on adjacent lands into account when designing and analyzing projects (cumulative effects analysis), but whether the FS should be required to compensate by managing at a higher standard when conditions on adjacent land(s) were low. There was also concern that high value elk habitat conditions and circumstances on private lands could justify a lower standard on adjacent NFS lands. The agency participants recognized that elk may use lands with limited or no hunting access differently than public lands that typically have higher levels of hunting pressure. For example, the importance of cover and security areas may be less on private land where hunting pressure and recreational use is lower, than on public land where hunting pressure and recreational use is generally higher. When the goal is to keep elk on public land, we would encourage consideration of conditions on all ownerships within the EAU, whether good or poor, when making decisions at the project level.

2. Ecological Context

The agency participants focused on elk habitat considerations in this effort. That being stated clearly, the group advocates for ecologically appropriate elk habitat management under the umbrella of landscape scale ecosystem management, which provides a range of habitats to support all fauna native to the landscape, including elk. This landscape scale ecosystem approach includes a complementary ecosystem and species specific approach (coarse filter/fine filter) to guide ecological restoration based on maintaining biological diversity.

Discussion:

The ecosystem component (coarse filter) includes a consideration of the composition, structure, ecological functions, disturbances, and habitat connectivity characteristics of an ecosystem. Providing habitat conditions across a landscape that are representative of those which produced and have sustained native fauna will generally provide for ecological integrity and biological diversity at a landscape scale. However, there may be circumstances where maintaining the appropriate habitat

requirements for a particular species at the appropriate geographic scale does not result in the species being present for reasons outside of the FS control (e.g. not habitat related).

The species specific component (fine filter) of this approach focuses on the critical habitat elements and limiting factors for a particular species, and may be focused more on human related disturbances rather than habitat. An example of a fine filter consideration is limiting human disturbances on big game winter range to prevent displacement or harassment.

With an effective ecosystem/coarse filter component in place, the more costly and information intensive species specific/fine filter approach can be focused on the few species whose requirements and circumstances may not be fully addressed by the ecosystem/coarse filter approach.

Habitat varies in space and time given the dynamic nature of ecosystems. This may be referred to as natural range of variation (NRV); FS 2012 Planning Rule (USDA-FS 2013). NRV is defined as the spatial and temporal variation in ecosystem characteristics under historic disturbance regimes during a reference period. The reference period considered should be sufficiently long to include the full range of variation produced by dominant natural disturbance regimes, often several centuries, for such disturbances as fire and flooding and should also include short-term variation and cycles in climate. Natural range of variation (NRV) is a term used synonymously with historic range of variation or range of natural variation. The NRV is a tool for assessing ecological integrity, and does not necessarily constitute a management target or desired condition. The NRV can help identify key structural, functional, compositional, and connectivity characteristics, for which plan components may be important for either maintenance or restoration of such ecological condition. Addressing departures from NRV (e.g. conducting treatments to increase aspen habitat if aspen habitat is underrepresented on the landscape), generally contributes to providing habitat conditions across a landscape that are representative of those which produced and sustained the fauna native to that landscape. Native species (including elk) evolved with, adapted to, and contributed to, natural disturbance patterns and the resulting mosaic of habitat conditions. The diverse needs of all species across a landscape require the consideration of habitat requirements over broad geographic areas and extended time periods.

Habitat restoration opportunities may exist where conditions have departed from those that provided for the species that are native and adapted to that landscape. Restoring the range of ecological conditions that sustained native species in the past will best conserve biological diversity and will maintain habitat for a broad range of species.

3. Winter Range Recommendation

Human disturbance on winter ranges should be minimized to prevent displacement or harassment of elk on winter range. In addition, the amount and types of available cover and forage should accommodate the needs of elk (within the bounds described in the ecological context section above) and take into consideration the limiting factor for elk on winter range.

At the project level, the various canopy cover classes of conifer cover on winter range will need to be examined relative to their potential benefit to elk.

Discussion:

The desired condition for winter range is to maintain elk use of NFS lands during the winter and early spring (approximately December 1 to May 15, but should be flexible to account for site specific conditions), in keeping with MDFWP 2005 Elk Plan and FS Forest Plan direction for multiple resources.

The agency participants agreed that winter range would either be updated at the project level by MDFWP for an elk herd or default to the delineations currently mapped by MDFWP and available on their website. MDFWP currently does not delineate or map 'critical/crucial' winter range separate from other winter range. It was recognized that in many areas very little winter range is found on NFS lands due to their relatively higher elevations and accompanying higher snow accumulations. Given that consideration, where NFS lands do provide winter habitat for elk, the agency participants defined a desired condition of providing maximum protection, by maintaining adequate forage and cover and by restricting travel for the objective of maximizing effective use of winter ranges on NFS lands by elk. Consistent with this idea, (but not generally considered by the FS in travel management), it was recognized that in a given local situation, special area closures may be warranted for motorized and non-motorized uses (precluding those activities such as snowshoeing or skiing), or at least a consideration of prohibiting cross-country or dispersed travel on winter range by designating travel corridors for both motorized and non-motorized recreation.

Both motorized and non-motorized routes should be examined for the potential to disturb and/or displace elk. Elk may be able to habituate to predictable, limited human travel when it is limited to a designated route (with associated area closures) through winter range, although there may still be physiological effects (Canfield et al. 1999; Cassier and Ables 1990). The location of routes should be examined as well. Relocation of routes may reduce impacts on elk, for example, by relocating an over-the snow motorized route away from key areas used by elk in severe winter conditions.

The literature suggests that forested cover on winter range may have multiple functions including snow interception, thermal modulation, wind buffering, and to provide areas that "hide" animals and provide security in the face of disturbance. The first two functions are provided by relatively mature forest stands with relatively high canopy cover (40-100%) (Carter 1984, Eon 2004). Thomas et al. (1979) suggested that thermal cover is coniferous trees at least 40' in height and 70% crown closure, but these numbers have not been validated experimentally (Skovlin et al. 2002).

Lyon et al. (1985) reported that east of the Continental Divide elk forage in grasslands during the winter, but seek cover in adjacent timber stands. The research summarized that logging in these forested stands will normally be detrimental to elk. West of the Continental Divide, Thompson et al. (2005) documented the importance of forage availability in the coniferous stands when snow conditions in the grasslands become crusty. The research recommended maintaining connected patches of denser canopies for snow interception, and to maintain some more open canopy conditions that result in "forested forage". Skovlin et al. (2002) also report that different stand conditions provide varying degrees of thermal protection and cover from snow. Myserud and Ostbye (1999), in their

discussion of all the important functions of cover for ungulates, distinguish between canopy cover, which shelters an animal from above, and ground cover, which is what hides an animal viewed from ground positions, which are both potentially important functions of cover on winter range. All that being said, elk populations can prosper in areas lacking a coniferous forest structure (Skovlin et al. 2002). In those situations, elk may use topography and aspect to regulate temperature (Beall 1974).

Cook et al. (1998) concluded that elk benefited more from forage than from cover in terms of overall fat metabolism through the winter. They concluded that thermal cover may be important under certain conditions, but its value is relational to other habitat attributes that contribute to the productivity of elk herds. The agency participants had an opportunity to discuss this research with staff from the Starkey Research Station. We concluded that the conditions under which the study was conducted, including the climate of the study area and the use of penned and fed elk, may not be applicable to winter conditions for free ranging wild elk on the four forests addressed in this document.

The agency participants ultimately agreed that elk may use cover in the winter for a variety of reasons that may include thermoregulation, but that forest cover may also be important in keeping forage available to elk in some situations (crusty, icy conditions, or deep snow for example), or to buffer elk from potential disturbances on winter ranges. MDFWP representatives pointed out that from an energy expenditure reduction standpoint, big trees and multi-layer canopies may provide benefits not provided by small trees or single layer forest canopies. The participants concluded that coniferous cover should generally be maintained on elk winter ranges within the capability of the landscape (see ecological context section). The agency participants also discussed the time it takes for conifer cover to become multistoried or dense-canopied, which is the kind of structure that provides snow interception following regeneration of forest cover (e.g. burning or timber harvesting) on winter range. Although the screening function may be recovered in about 15-20 years, the structural conditions that provide for snow interception may not recover for 60 years or more.

Fire suppression for the last several decades has changed the way fires burn. Fire exclusion has resulted in a more homogeneous landscape with an increased potential for larger stand-replacing fires (Arno and Bunnell 2002, Hessberg et al. 1999, Quigley et al. 1996). This is especially applicable in warm, dry low-elevation forests (the types of forest that provide elk winter range) where frequent low-intensity fires were the norm. Many of these forests are now unnaturally dense. Furthermore, as more homes are built in the wildland urban interface, there is a greater social demand for fire suppression at the same time that the risk of fire has increased. While maintaining multi-layered canopies may be beneficial for elk on winter range, the group recognized that treatment of hazardous fuels in areas where winter range overlaps with a wildland urban interface may trump the needs of elk.

After the 2000 wildfire season, which burned a substantial amount of NFS lands (as well as other lands), the Forest Service re-examined wildland fire policies. As a result, several documents were developed that set goals for wildland fire policies. Congress subsequently passed the Healthy Forests Restoration Act in 2003 which further emphasized the need to manage hazardous fuels. In conclusion, forested cover is an important consideration on elk winter range; however, the national attention and emphasis on reducing hazardous fuels to protect communities, watersheds, and other at-risk values may result in management activities that affect winter cover. This effect could be mitigated if ungulate cover needs are considered in the design of hazardous fuels projects. The agency participants

concluded that any potential conflict between managing for cover on elk winter range and the potential need for hazardous fuels reduction would be best resolved at the project level.

In addition to looking at the energy conservation aspects of winter range related to reducing disturbance impacts and having sufficient forest cover, we also discussed the importance of forage quality and availability for elk using winter range areas on NFS lands. In recognition of this desire, the agency participants outlined some situations where it might be desirable to allow some level of timber harvest and/or fire, recognizing that there may be situations where an increase in non-conifer vegetation (often to enhance quantity or quality of ungulate forage) are determined to be beneficial to elk or other wildlife species on winter ranges.

In conclusion, there will be situations where multiple use considerations (other than elk) and human safety will drive vegetation management on winter range, or where vegetation management affecting coniferous cover may be recommended on winter range to benefit elk or other species. Examples include:

- For research studies
- For conifer removal in aspen stands to promote aspen regeneration
- To remove conifers from areas that are desirable as grassland or shrubland areas; these are generally smaller trees on the edge between an opening and a coniferous forest and are generally considered as areas of conifer colonization
- For safety reasons such as fuel reduction around dwellings and/or administrative sites, and/or hazard tree removal along roads
- To conduct hazardous fuels reduction projects within the wildland urban interface aimed at protecting communities, and other values at risk (e.g. campgrounds, municipal watersheds) from catastrophic wildfires. To the extent practicable, integrate wildlife habitat considerations in project designs.
- For situations where the removal (salvage) of dead trees has a benefit to elk in the long-term (forage production/movement/recovery of the stand)
- To improve elk forage where forage has been determined to be limiting rather than cover

4. Security Area Recommendation

The agency participants recommend that forest management activities involving access management (e.g. travel planning; vegetation projects requiring temporary or permanent road construction) provide adequate security areas to allow elk to remain on NFS lands during the archery and rifle hunting seasons. Lyon and Christensen (1992) defined security as "the protection inherent in any situation that allows elk to remain in a defined area despite an increase in stress or disturbance associated with the hunting season or other human activities". They defined security areas as "any area because of its geography, topography, vegetation, or a combination, that will hold elk during periods of stress." We suggest that the local MDFWP and FS wildlife biologists work together to define the numerical parameters (i.e. size of area, distance from roads, percentage of analysis unit, etc.) to be used for determining security areas at the local project level. Concepts from the "Hillis Paradigm" (Hillis et al.

1991) can be used to guide this process. For FS and MDFWP purposes, the analysis unit is the EAU, as described in section 1. We suggest a consideration of the following in the security discussion:

- In regards to elk security, the period September 1 – October 14, i.e. for the archery season, in addition to the standard October 15 – November 30/December 1 time period, i.e. the rifle season should be considered relative to public routes used by any motorized vehicle. Consistent, frequently-used non-public routes or temporary roads that are used during hunting season(s) would also need to be included in any security analysis. Thresholds for consistent, frequent use of these roads are to be determined based on site-specific considerations and discussions between local biologists from both agencies.
- Security areas should be well-distributed within the EAU (not all concentrated at high elevations or in wilderness) to account for movements due to weather and to help maintain good elk distribution on NFS lands throughout the hunting season. Generally high elevation areas that are above tree-line or steep ($\geq 80\%$ slope) areas that are not used by elk will generally not be considered elk habitat. However, at the project level, there may be examples where steep or cliff-like areas may serve to deter hunters and therefore contribute to security.

When the amount and arrangement of motorized routes has been determined to be a limiting factor in a given situation, and when security areas on NFS are not adequate to maintain elk use of NFS lands through the expected fall time period (until weather triggered migration events), as deemed through discussions between the two agencies (discussion to include whether other factors are affecting how elk use an area), MDFWP and FS biologists should jointly develop specific recommended strategies to address the situation (including the use of Hillis et. al. 1991 concepts). Recommended habitat management strategies may include the use of seasonal road closures (9/1 or 10/15 depending on the individual situation) to increase area specific elk security levels, managing for a higher percentage of the EAU that provides security (e.g. 50%, etc.), increasing the minimum size of security areas (e.g. 500 acres, etc.), and/or increasing the minimum distance of the security areas from open motorized routes (e.g. 1 mile, etc.). To be effective, project activities related to travel management would need to be designed to address these specific strategies.

Discussion:

Security areas are intended to reduce elk vulnerability during the elk hunting season, and to provide animals the opportunity to meet their biological needs without making large range movements (e.g. to private land where hunting is not allowed or to lower quality habitats) (Lyon and Canfield 1991). This also allows for a more ethical, fair chase hunting experience, and for the hunting public to have the ability and real opportunity to effectively hunt and harvest a public resource on public lands. Maintaining elk on public land also contributes to wildlife viewing, other values, and ecological roles (e.g. herbivory, predator prey dynamics, a source of carrion, etc.).

MDFWP biologists advocated that the 'hunting season' include the archery season as well as the general rifle season in regards to analyzing security levels. They cited a consistent increase in the number of archery hunters (doubling between 1990 and present) and subsequent increased levels of

motorized use during the archery season. MDFWP's elk security concerns depending upon the individual situation relate to: 1) bull elk survival during both the archery and rifle season in some cases; 2) elk distribution during the hunting season (i.e. are elk being pushed into marginal habitats that may negatively influence survival and reproduction); and 3) availability of elk, particularly antlerless elk, on NFS land (i.e. potential displacement to private land or checker-boarded areas of NFS ownership where access to NFS land is limited or unavailable, or into only generally inaccessible areas on NFS land) during the fall hunting season. The last concern is particularly important prior to the opening of the general rifle season when the overwhelming majority of antlerless elk harvest for population control occurs.

As such, fall elk security levels should be assessed either just using the September 1 starting date or both the September 1 and October 15 hunting season related starting dates, rather than just running an analysis using October 15 as the starting date, as has often just been done in the past.

The concept of security areas is embodied by the "Hillis paradigm", a paper compiled by Hillis et al. in 1991 as part of an elk vulnerability symposium proceeding. Hillis et al. recommended identifying security areas within the hunting season home range. In practice on these four National Forests, elk have the potential, depending on weather and other conditions, to use the entire breadth of elevations within their home range during the big game archery and general rifle hunting seasons. Therefore, it is not necessary or possible to identify a consistently "separate" fall use area within an EAU.

Hillis et al. recommended identifying areas at least ½ mile from an open motorized route and at least 250 acres in size as the minimums for providing adequate security. The authors cautioned that in some cases, distance from open routes and the size of security area blocks must be increased (e.g. 350 acres >= 1 mile from an open motorized route) to provide adequate security. Hillis et al. recommended that at least 30% of a valid analysis unit be comprised of security areas.

Although Hillis et al. (1991) define security as "non-linear blocks of hiding cover", they also suggest that effective security areas may consist of several different cover types if the block is relatively unfragmented. Relative to the composition of the security areas, there was discussion about whether Hillis et al. (western Montana) was applicable to these four National Forests.

The agency participants spent a fair amount of time discussing the definition, distribution and vegetative composition of security areas. MDFWP biologists felt that security areas are not meaningful to elk, if by virtue of the physical conditions of the landscape (rocks, cliffs, steep areas) elk would not be expected to use them to meet their biological needs. To be most effective, security areas should be well-distributed cross the breadth (geographic and elevations) of elk habitat within the EAU. This is especially relevant where a portion of the home range is relatively inaccessible such as represented by sanctioned wilderness areas.

The studies considered by Hillis et al. were done in areas where forests of various ages were continuous. In their discussion of security areas, Christensen et al. (1993) speak to the significance of cover in this equation and note that where cover is ubiquitous, security can be controlled by road management alone. They recommend that detailed analyses of hiding and thermal habitat components

are not essential relative to security areas and that a consideration of coniferous cover is important for more than just elk vulnerability and therefore should be assessed at a landscape level to develop long-term perspectives to address the condition, quantity, location, and configuration of cover (see ecological context section and spring-summer-fall cover section).

In contrast to the Hillis et al. study areas, the landscapes on these four National Forests include many areas of more open habitat or where forests and grasslands are interspersed in a mosaic. A break out group of agency participants discussed the cover and security area relationship and concluded that consideration of the quantity and quality of forested cover at the scale of the non-winter portion of the elk analysis unit would be better than defining security areas as "blocks of hiding cover". This also allows for the situation where areas naturally include a mosaic of forest and/or open habitats, but which operationally are secure. In addition, recent analyses of elk habitat selection during the hunting season in Montana (Proffitt et al. 2012 and personal communication with Kelly Proffitt, MDFWP) did not show a significant selection for security areas comprised of total conifer cover relative to security areas just defined by size and distance from a road. In addition, Proffitt's analysis showed that security areas as a variable in habitat selection during the hunting season are strongly related to the motorized route variable.

Hillis et al. only speak to "open roads" and "closed roads". They suggest that hunting pressure is concentrated along open roads, but that (hypothetically) closed roads located within security areas may increase elk vulnerability by providing walking and shooting lanes. Unsworth and Kuck (1991) note that road closures may have varied effects on animal distribution and hunter use and success. They cite to several studies where road closures allowed elk to remain in more preferred sites for longer periods of time (Irwin and Peek 1979, Marcum 1975). Basile and Lonner (1979) reported that when vehicular travel was restricted, hunters spent more time walking, saw more elk, and had greater success and reported having a higher quality hunting experience. Based on these studies and the recent review from McCorquodale (2013) on elk and roads, the agency participants agreed that Hillis et al. recommendation to "minimize" closed roads within security areas was not necessary.

The agency participants noted that there has been a dramatic increase in all-terrain type vehicles, and therefore agreed that all FS system routes that receive any kind of motorized use by the public should be considered for their impact to elk not just open 'roads'. A review of the scientific literature regarding elk, roads and traffic (McCorquodale 2013) provides strong evidence that elk use declines as traffic volume increases (Johnson et al. 2000, Edge and Marcum 1991, Rumble et al. 2005, Stubblefield et al. 2006, Montgomery et al. 2013). Johnson et al. found that elk avoided roads that had 2-4 vehicles per 12 hours or higher.

Given this threshold for avoidance, agency participants agreed that closed routes or low intensity, occasional private or administrative travel and management activity on routes closed to the public could be reasonably excluded in identifying security areas. However, consistent, frequently-used non-public routes or temporary roads would detract from security areas, if such roads are used during hunting season(s).

The agency participants recognized that there were a lot of different variables that must be considered when applying the parameters from the Hillis et al. paper, and as the paper suggests, the numerical

recommended guidelines may not be sufficient in all cases and that **“strict adherence to the guidelines should be avoided”**.

One of the driving factors in the security area discussion was to try to reduce or eliminate elk displacement from public land prior to normal migration events. The objective of maintaining or enhancing elk presence on NFS lands so that elk are available to the hunting public on public land should be considered in the determination of the specific parameters (block size, distance from motorized routes) used to identify security areas, in the percentage of the EAU dedicated to security areas, and in discussions involving hunting season related seasonal road closures. Additionally, it was recognized that elk may use habitat differently on private lands than on public lands. For example, the importance of security areas may be less on private land where hunting pressure and recreational use is lower, than on public land where hunting pressure and recreational use is generally higher. The agency participants recognized that increasing elk security alone on NFS land may not be enough to maintain elk use of NFS land.

The agency participants felt strongly that posted private land was not the desired way to provide security for elk that also use FS lands, as that situation results in lost opportunity for the general public and decreased or lost management effectiveness relative to population control. In addition, when elk are displaced to private land, it negates any intentional elk –related management decisions by the FS. The agency participants recognized that although it isn’t desirable for posted private land to act as security for elk using public lands, elk may choose that form of security. There was discussion regarding whether or not elk would re-occupy public land after displacement to private lands where hunting is not allowed regardless of potential management actions by the FS and/or MDFWP. We concluded that increasing security and habitat quality are important and necessary considerations, but that some elk herds may, through learned behavior, continue to use private lands regardless of conditions on public lands. This would need to be addressed outside of habitat management and hunting seasons on NFS lands. For example, there may be access incentives available for private landowners to consider.

The agency participants recognized that given high enough levels of hunter numbers and hunting pressure, security areas may not be effective, resulting in elk being displaced to other areas including private land (Vales et al. 1991; Lyon and Christensen 2002). It may be determined through the course of discussions between the two agencies that non-habitat related management actions outside of USFS control (such as a hunting season related change) may be necessary to address elk distribution and displacement issues, if habitat management actions alone are insufficient, with the recognition that any hunting season related change would have to go through MDFWP’s public Commission process. Given that both land use (i.e. travel plans) and hunting seasons can represent significant public values and expectations, it is recognized that changes to either can be procedurally difficult and contentious. It is also recognized that each has its own process and that elk distribution issues need to be responsibly addressed by both. Working together, both agencies would need to assess the relative management gains represented by different FS and MDFWP management options and not unilaterally rely upon the other’s actions or dismiss the potential for making changes that would increase the potential to maintain elk on NFS lands.

The group acknowledged that the FS multiple use mandates may result in lower than desired elk security levels in some areas, particularly during the archery season. Where travel management decisions have already been made, and consideration was given to elk security in the overall decision, elk security analyses at the project level should (1) focus on any additional temporary motorized routes and their potential to reduce elk security and (2) include potential mitigation opportunities to enhance elk security including but not limited to date changes to existing open motorized routes. The potential to revisit existing travel plans in order to improve elk security where needed should remain an option.

5. *Habitat Effectiveness Recommendation*

Habitat effectiveness is defined as the percentage of available habitat that is usable by elk outside the hunting season (Lyon and Christensen 1992). For areas intended to benefit elk summer range and retain high elk use, habitat effectiveness related to motorized routes should be 70% or greater. For areas where elk are one of the primary resource considerations habitat effectiveness should be 50% or greater. In situations involving elk summer range where habitat effectiveness is less than 50% elk use potential (which equates to an open motorized route density of about 2 miles/square mile (Christensen et al. 1993), these areas must be recognized as making only minor contributions to elk management goals (Christensen et al. 1993). We recognize that due to the USFS's multiple use mandate that there will be areas that are managed for habitat effectiveness of less than 50% elk use potential. At the project level an elk habitat effectiveness analysis should be conducted. In those areas where there is a desire to improve and/or maintain elk habitat use, we recommend maintaining or decreasing road densities that correspond with the desired habitat effectiveness level per Christensen et al. (1993).

2 mi/sec
= 50%

Travel planning should also take into consideration the location of motorized routes and minimize motorized use in highly productive elk summer range habitats (see discussion).

For simplicity, route density is used as the proxy for habitat effectiveness. In reality, elk habitat effectiveness may be influenced by other factors than motorized routes. Other factors should be considered at the site-specific project level.

Discussion:

A desired condition expressed by the agency participants was to maintain elk use of National Forest land during the highly productive summer months (per Canfield et al. 1999). This recommendation focuses on elk distribution and is related to effective use of habitat for optimal fat accumulation on summer range (the time of year when forage conditions allow for weight gain needed to survive the winter and other stresses (such as the rut, and/or calf production and recruitment). Habitat effectiveness is defined as the percentage of available habitat that is usable by elk outside the hunting season (Lyon and Christensen 1992). This is the measure of success in meeting elk needs on summer range. Habitat effectiveness is directly related to motorized route densities (Christensen et al. 1993), but route locations may also be important. Recent studies (e.g. Wisdom et al. 2004; Proffitt et al. 2012) validate Lyon's (1983) finding that elk avoid open motorized routes and therefore, areas with high motorized route densities have the effect of reducing the available habitat. At 2 miles/section, elk use potential is about 50% (see **Appendix B**).

The agency participants acknowledged that not all FS lands would be managed with elk as the sole or primary consideration. The agency participants also acknowledged that travel management decisions often have to strike a balance between resource protection, public recreation opportunities, and other multiple use considerations. However, the potential to revisit existing travel plans in order to improve elk habitat effectiveness where there are concerns should be considered.

Where travel management decisions have been made, and consideration was given to habitat effectiveness in the overall decision, habitat effectiveness analysis at the project level should focus on the additional temporary project routes and their potential to reduce elk use of important summer habitat.

Although Christensen et al. (1993) suggest that any motorized vehicle use on roads will reduce habitat effectiveness, a review of the published literature provides strong evidence that elk use declines as traffic volume increases (Johnson et al. 2000, Edge and Marcum 1991, Rumble et al. 2005, Stubblefield et al. 2006, Montgomery et al. 2013). Johnson et al. found that elk avoided roads that had 2-4 vehicles per 12 hours or higher. Rowland and Wisdom (2012) also found that the strongest predictor of elk use in late summer was distance to open public roads. Therefore, low intensity, occasional administrative travel and management activity on routes closed to the public could be reasonably excluded in habitat effectiveness analyses. However, consistent, frequently-used non-public routes or temporary roads would detract from habitat effectiveness if such roads are used during the summer. The specific situation should be addressed at the project level and needs to be interpreted relative to potential for displacement of elk (see Lyon et al. 1985).

The group acknowledged that HE is an average condition, and that a range of habitat effectiveness can occur over a landscape. Some areas will have fairly homogenous route systems; other areas will have concentrations of open routes. In those situations, it is important to manage some areas with seasonal or yearlong restrictions such that route density is close to zero (100% habitat effectiveness).

The location of motorized routes may potentially negatively impact elk habitat as much as actual motorized route densities. Travel planning should consider minimizing or restricting motorized use on routes that impact high quality habitat, such as heads of drainages, saddles, moist areas, wet meadows, etc. (Lyon et al. 1985, page 7), and other important foraging habitats (e.g. aspen, riparian, grassland meadows, shrublands).

6. Recommendation for Spring/Summer/Fall Forest Cover

The recommendation is that within the non-winter portion of the EAU, coniferous cover will be managed within the ecological context or NRV for the geographic area (e.g. mountain range) where the EAU is located (see ecological context section). Cover assessments conducted for a project level analysis within the EAU should include a consideration of the condition (health), quantity, location, and configuration of desirable cover conifer species (see discussion). Specific to elk, the amount and types of available cover should accommodate the needs of elk relative to an assessment of limiting habitat factors (forage, cover) within the EAU.

Discussion:

The agency participants discussed the need to have any restrictions regarding cover management for elk, given the lack of research regarding the quantity of cover that is optimal. Additionally there is the general trend on the four forests (since the Forest Plans were written) of less timber harvest overall, smaller timber sales, and greater cover retention in treated areas (thinning rather than clear cutting). In addition, fire suppression has probably resulted in more cover than would be supported under a more natural fire regime. However, the agency participants recognized that the timber harvest levels could increase in the future and that large forest fires could significantly change the amount of available timber cover on any landscape in the future.

Current cover requirements in Forest Plans distinguish between cover for hiding and cover needed for thermal regulation. While we recognize the importance to elk of having cover available that provides hiding and/or thermal regulation benefits among other attributes, the agency participants did not see the need for managing for two different types of cover with different definitions. We did, however, recognize value in differentiating between the functions of cover on winter vs. spring/summer/fall ranges. We agreed that generally both hiding and thermal functions on spring-summer-fall ranges could be provided by conifer stands with at least 40% canopy cover (as determined from available map products). Other functions of cover on spring-summer-fall range (e.g. forested foraging areas) could be satisfied with lower canopy cover stand conditions.

A previous interagency group that discussed management direction for elk in 2004 concluded that travel management and forage production were more important as management emphases to elk, and that cover is naturally dynamic relative to fire and the levels could be managed within natural fire regimes on most elk range. They felt that cover, where it occurred on elk winter range, was critical and should be maintained (Firebaugh et al. 2004). For this current effort, agency participants acknowledged that forested cover could function to reduce elk vulnerability during the hunting seasons; otherwise, forested cover may influence the way animals use habitat, and the ability of habitat to meet elk needs for growth and welfare requirements (Christensen et al. 1993). For example, Rowland and Wisdom (2012) found that late summer forage quality for elk in the Blue Mountains was highest where it was within a forest cover type. ✓

The agency participants discussed instances where forest cover was important for holding elk on public land even when security (due to route density) was lacking. The agency participants agreed that there may be legitimate reasons to maintain more cover in certain situations while reducing cover in other situations depending on the management issues in question. We ultimately agreed that it would be best to manage cover levels with respect to the ecological context of the geographic area (e.g. mountain range) in which the EAU occurs (see ecological context section).

The function of cover during spring, summer and fall may include thermal regulation, lengthening the season of succulence and palatability where adequate understory forage exists and the overstory provides shades, seclusion, and buffering of special features such as licks and moist areas (Christensen et al. 1993). Forested cover influences the way animals use habitat, and the ability of habitat to meet elk needs for growth and welfare requirements (Christensen et al. 1993).

In some areas, juniper, limber pine, whitebark pine, or ponderosa pine may function as cover for elk, but agency participants agreed that thinning or removal of these species may have more value, in the

larger ecosystem picture, than to manage them as sustainable cover for elk. The exception would be for the Ashland and Sioux Ranger Districts on the Custer NF where ponderosa pine is the primary tree species.

Forest cover is renewable. In other words, if cover is removed by fire or by timber harvest, it can regenerate with seedling trees naturally, or it can be planted with seedlings. To assess cover in an elk analysis unit, burned and harvested areas must be assessed and sorted into either baseline-non-functional cover or included as existing cover. Regenerated cover stands which are about elk height (4.5') high and $\geq 40\%$ canopy cover can function as hiding cover.

Ponderosa pine occurs on all 4 forests, but is the primary conifer species on the Ashland and Sioux Districts of the Custer National Forest. Ponderosa is more naturally open grown than other conifer species. On these 2 Ranger Districts, where ponderosa pine is the primary forest type represented, field validation showed that stands with at least 40% canopy cover consistently functioned to meet the hiding cover definition (90% of an elk at 200 feet distance). Stands with canopy cover of at least 25% were often sufficient to function to screen elk in conjunction with undulating topography (Canfield 2012).

Based on other field studies (Canfield 2011; unpublished data on Helena NF) and Lonner and Cada (1982), spring-summer-fall cover is provided by tree species or species mixes (occurring on these four national forests) that are naturally capable of having relatively dense ($\geq 40\%$) canopy cover, and could include Douglas fir, subalpine fir, spruce, and lodgepole pine. In eastern Montana (and South Dakota) ponderosa pine is the dominant cover type and is capable of having at least 40% canopy cover. These cover types or mixes of them will generally provide screening for animals and be capable of hiding 90% of an elk $\leq 200'$.

At the project level, additional considerations can be analyzed and field validated. For example, forested stands impacted by disturbance such as fire or insects and disease that had $\geq 40\%$ green canopy cover, but which currently have a high proportion of standing dead, may still function as hiding cover. Viewing angle may affect the functionality of cover in steep cutover areas (Canfield et al. 1986). Local topography can interact with vegetation to screen animals. Similarly, tall shrubs and/or downed woody material could also function to screen animals in some situations.

We concluded that a specific quantifiable cover recommendation was not supported by the scientific literature. While Lyon et al. 1985 (Coordinating Elk and Timber Management; 1985) speaks to "good cover" as being two-thirds of the total area, and Thomas et al. (1979) recommended managing for 40% cover and 60% forage for elk, to our collective knowledge, these recommendations have never been empirically tested. Blocks of forested cover were not a strong predictor of elk distribution in a recent study in Montana (Proffitt et al. 2012).

7. Big Game Cover Patch Size Recommendation

There is no minimum patch size (for forested cover) recommended. Recognition should be given at the project level to the site specific big game use patterns relative to patch size.

Discussion:

Agency participants discussed the distribution of forested cover, and whether or not there was a desirable minimum cover patch size. A research paper from Colorado (Wait and McNally 2004) identified 10 acres as a minimum cover patch size for that area, while a paper from the Blue Mountains area of Oregon (Thomas et al. 1979) recommended minimum patch sizes based on 4-8 sight distances (200') resulting in patches of 6.5 – 26 acres. We concluded there was no defensible specific minimum patch size for cover, but that there are circumstances when very small patch sizes or timber stringers might be important (but may also function as “linear traps” as hunters may recognize these as travel lanes; Lyon, email communication; March 2012), and that they should be identified at the project level. For example, habitat for a particular elk population may be inherently open and linear forested patches in draws may be very important to maintain.

8. Forage Recommendation

While, there are no specific quantifiable recommendations relative to forage quality or quantity resulting from the current effort, agency participants recommend the following desired conditions relative to forage:

- On NFS lands, high quality and abundant forage will be available for big game throughout the seasons.
- Maintain a diversity of native forbs, grasses, and shrubs that are well distributed. Maintain a variety of successional stages, as well as key ungulate forage habitats such as riparian, aspen, grassland, sagebrush and other shrublands. Forage needs should be considered for all seasonal ranges.
- Grazing allotment plans should take into consideration the need for available high quality and abundant forage for big game, as well as the forage needs for domestic livestock where the species co-occur.
- During annual coordination meetings between MDFWP and FS, areas of concern relative to the availability, amount or quality of forage for big game will be considered, with the intent of developing specific strategies that may include modification of livestock grazing, modifications to motorized travel plans to address disturbance impacts, habitat improvements using prescribed burning, wild fire, timber removal; restoration of native plants, and/or invasive weed control.

Discussion:

Recent studies continue to support the importance of forage for elk and its effect on their use of a landscape (e.g., Rowland and Wisdom 2012). High quality forage is typically high in both carbohydrates and protein.

Local circumstances result in varying effects on elk (e.g. elk in Arizona may experience a very different habitat reality than elk in Montana). On NFS lands in the Northern Region, elk are coming out of the most forage restricted time of year in the spring, are in the last trimester of pregnancy, and are beginning to nurse. Summer forage is key to abundant milk production as nursing of the growing calf continues. Summer is also the time of year when fat reserves are accumulated, which affect breeding success, pregnancy rates, parturition synchronization, the energy to avoid predators in the winter, and general winter survival (physiological demands of cold temperatures, travelling in snow during a time of greatly reduced forage availability and quality). Fall forage provides some maintenance energy between the summer and the winter when fat reserves supply much of their energy. Fall forage also helps bulls recover from stress and energy expenditures associated with the breeding season. Winter forage provides some maintenance energy and roughage for rumination which produces body heat. In addition, protein levels in some shrubs may be sufficient even in winter to meet elk protein requirements.

High quality forage is often found in areas with limited coniferous cover (e.g., meadows, brushfields, and aspen stands). Riparian and wetland areas can provide disproportionate amounts of succulent vegetation (particularly in more arid conditions). Forests can also provide important forage, particularly where they are open enough to allow adequate sunlight, water, and nutrients to get to the forest floor. Forage within forested areas can have a longer green and succulent season, when more open areas cure out in the late summer sun.

Any management action affecting vegetation can affect forage quality and abundance (e.g., wildfire management, fire suppression, prescribed fire, thinning, timber harvest, noxious weed management, livestock grazing, and revegetation). Management actions related to motorized vehicles or even non-motorized uses which disturb or displace elk can affect the ability of elk to utilize available forage.

Factors such as fire suppression, noxious weeds, or some livestock grazing practices can alter vegetative composition, structure, and successional stage. Forage can often be produced or improved by addressing the departure from range of natural variation of vegetative composition and structure (e.g., fire management, mechanical treatments, improved livestock management, aspen or riparian treatments, and noxious weed treatment). Habitat management projects designed to address departure from NRV generally benefit a broad suite of fauna adapted to that landscape.

The main focus in this collaborative effort is on travel management and cover requirements for big game. However, agency participants agreed that at some future time, management of forage would need to be addressed in some detail. However, that discussion would need to include other FS and MDFWP specialists.

The agency participants recognized that forage availability and quality plays a critical role in big game habitat use and big game distribution. It was also recognized that more importance should be placed on forage availability and quality during the summer and early fall, as that is often the determining factor in whether or not animals make it through the winter (Canfield et al. 1999) and the effects on body condition during the rut likely influences other factors such as pregnancy rates and synchronized calving. High quality forage may be seasonally unavailable in some areas due to

forest succession, conifer encroachment into foraging areas, domestic livestock grazing, or noxious weeds, fire suppression/altered fire regimes, altered vegetative successional pathways, aspen loss due to a variety of factors, etc.

Declines in foraging habitat quality may be particularly negatively impacting species such as mule deer and moose. Motorized and non-motorized recreation, nonhuman predators, and other factors can disturb and displace elk and other big game from high quality foraging habitat. It was also determined that future discussions, whether it be at the planning level or the project level, will need to address the issues related to prescribed burning and management of species such as big sagebrush and juniper species.

9. Elk Parturition/Nursery Areas

The recommendation is to avoid activities that disturb known calving areas during the birthing period (generally from May 15 to June 30). In areas where brucellosis is a concern, delineating calving areas will be an emphasis from the standpoint of maintaining spatial/temporal separation with domestic livestock.

Discussion:

Although not all the eastside forests have calving areas mapped, the agency participants felt it was important to provide security and structural habitat features to maintain elk use of birthing areas. There were discussions about whether protection of calving areas was needed and about the areas and types of habitat used by elk for calving/nursery areas.

There were examples provided by agency participants where elk used the same general areas every year for calving, and other examples where calving was variable depending on weather and snow conditions. Instead of developing a very specific recommendation, the agency participants decided that it might be best to address this issue on a case by case basis at the project level depending upon whether or not the Forests or MDFWP had mapped calving/nursery habitat, or if the project area is within an area that may be used as an elk birthing area due to its elevation and habitat type.

10. Migration Corridor Recommendation

There are no specific, quantifiable recommendations for elk migration corridors. Project level discussions between the two agencies should take into consideration provision and/or maintenance of security and structural habitat features for landscape connections where they can be identified.

Discussion:

The agency participants discussed whether or not specific migration corridors could be identified. Telemetry data has shown some traditional use of seasonal migration routes. There was interest in maintaining not only seasonal migration routes but also dispersal routes that maintain landscape connectivity.

OTHER BIG GAME SPECIES RECOMMENDATIONS

At the project level, consultation between the FS and MDFWP should include specific consideration to the habitat and security needs for other big game species such as mule deer, white-tailed deer, moose, bighorn sheep, and mountain goats, as needed.

In regards to bighorn sheep, the FS should work collaboratively with MDFWP to explore opportunities for re-establishment of bighorn sheep and/or maintenance of existing bighorn populations. The forage recommendation above in this document provides some general guidance for bighorn foraging habitat, recognizing that bighorn foraging areas are much more limited in extent than for elk and generally have some proximity to escape terrain, and that setting back vegetative succession can improve visibility and improve their ability to detect and escape predation. In addition, the following guidelines, specific to bighorn sheep, are recommended (WAFWA 2007):

- Manage domestic sheep or goat grazing to achieve effective separation, reduce risk of association, and avoid range overlap with wild sheep.
- Ensure annual operating instructions (AOIs) issued to grazing permittees include measures to minimize association and identify strategies to deal with stray domestic sheep or goats.
- Develop and use of Best Management Practices (BMPs) to reduce straying by domestic sheep or goats.
- Manage wild sheep habitat to promote healthy populations in areas away from where domestic sheep or goats are permitted.

Discussion:

Given time constraints, the agency participants focused almost entirely on elk. Generally, it was agreed that recommendations developed for elk would often benefit species such as mule deer, moose, etc. However, we recognized the need for caution in being "elk centric" as at times that may not benefit other species, and that recommendations specific to other species might be necessary. For example, recommendations for bighorn sheep which have experienced recent die offs, and which were recently listed by the Regional Forester in the Northern Region as "Sensitive" are included.

The agency participants recommend that the project level is the best option for dealing with habitat issues specific to other species.

CONCLUSIONS

These collective recommendations reflect many hours of deliberation and discussion, literature reviews, and conversations with elk researchers. New research will continue to contribute to the way we view elk and elk habitat management. These recommendations should be periodically reviewed and updated to reflect “best science” and the most current information.

For example, in western OR and western WA (Rowland and Wisdom 2012), a variety of analyses of radio-telemetry data from different study areas showed that in resource selection modeling four variables accounted for the large majority of elk use. These four covariates consistently ranked highest for elk use across 5 study areas/years and when applied to independent landscapes, showed an almost perfect correlation of elk predicted versus observed use. The four covariates were:

- elk dietary digestible energy (higher nutrition, higher use)
- distance to roads open to public access (farther from roads, higher the use, out to 4 km; this covariate also could include trails open to public motor uses)
- percent slope (flatter the slopes, higher the use)
- distance to cover-forage edges (closer to edges, higher the use)

This modeling process has more recently been used as a template for the Blue Mountains work, and a Blue Mountains summer range model (Rowland and Wisdom 2012) is now available. The Blue Mountains are more similar to the four eastside forests that participated in this collaborative effort. There were four variables that predicted elk habitat use for late summer:

- elk dietary digestible energy (higher nutrition, higher use)
- distance to roads open to public access
- % slope (highest use at moderate slope classes)
- % forested vegetation

MDFWP is working with FS Research to explore the potential application of any Blue Mountains model to Montana and to evaluate the potential of testing the performance of the model with data from Montana; see **Appendix C** for the highlights of this discussion.

Project Recommendations for Migratory Bird Conservation
U.S. Fish and Wildlife Service, Utah Field Office (May 2020)

The Migratory Bird Treaty Act (MBTA) is the cornerstone of migratory bird conservation and protection in the United States. The MBTA implements four treaties that provide for international protection of migratory birds. The USFWS maintains a list of all species protected by the MBTA at 50 C.F.R. § 10.13. This list includes over one thousand species of migratory birds, including eagles and other raptors, waterfowl, shorebirds, seabirds, wading birds, and songbirds. The MBTA does not protect introduced species such as the house (English) sparrow, European starling, rock dove (pigeon), Eurasian collared-dove, and non-migratory upland game birds.

The U.S. Fish and Wildlife Service (USFWS) recommends that the following migratory bird conservation measures be implemented as you complete your project:

- a. Wherever possible we recommend that projects be completed outside the migratory bird nesting season to avoid and minimize impacts to migratory birds.
- b. If the project includes the loss or degradation of migratory bird habitat then complete all portions of the project that could impact migratory birds outside the maximum migratory bird nesting season. This includes ground-disturbing activities, habitat removal, clearing or cutting of vegetation, grubbing, burning, etc. If that is not feasible, we recommend that you complete the project outside the minimum migratory bird nesting season.

The time period associated with the maximum migratory bird nesting season is approximately December to August. The time period associated with the minimum migratory bird nesting season is April 1 to July 15 (time-frame when the majority of annual bird nesting occurs).

- c. If the project needs to occur during the migratory bird nesting season, impacts to birds can be avoided or minimized by completing vegetation treatments and vegetation clearing and removal actions during the fall and winter (outside the migratory bird nesting season per above) prior to the nesting season when the project will begin.
- d. If a project may impact migratory birds and/or cause the loss or degradation of migratory bird habitat, and such work cannot occur outside the migratory bird nesting season, we recommend surveying impacted portions of the project area to determine if migratory birds are present and nesting. Surveys should emphasize detecting presence of USFWS Birds of Conservation Concern, take place during the nesting season the year before the nesting season in which project is scheduled to occur, and should document presence of migratory birds at least throughout the entire minimum migratory bird nesting season (April 1 to July 15). Nest surveys should be conducted by qualified biologists using accepted survey protocols.
- e. If your project must occur during the maximum migratory bird nesting season, implement measures to prevent migratory birds from establishing nests in the potential impact

area. These steps could include covering equipment and structures and hazing birds away from the project footprint. Migratory birds can be hazed to prevent them from nesting until egg(s) are present in the nest. However, we acknowledge that hazing migratory birds away from a project site is likely only practical for projects with a relatively small footprint (i.e. projects about 5 to 10 acres in size or smaller). Do not haze or exclude access to nests for bald or golden eagles or any migratory bird species federally listed under the Endangered Species Act (ESA), as these actions are prohibited without a permit for these species.

- f. If your project must be scheduled during the maximum migratory bird nest season, and vegetation clearing and removal work cannot be completed prior to the nesting season, then we recommend performing a site-specific survey for nesting birds no more than 7 days prior to all ground-disturbing activities or vegetation treatments.

If you document active migratory bird nests during project nest surveys, we recommend that a spatial buffer be applied to these nests for the remainder of the nesting season. Vegetation treatments or ground-disturbing activities within the buffer areas should be postponed until after the birds have fledged from the nest. A qualified biologist should confirm that all young have fledged.

We recommend the use of the *Utah Field Office Guidelines for Raptor Protection from Human and Land Use Disturbances* (Romin and Muck 2002) to provide consistent application of raptor conservation measures to your project or action in Utah. We provide recommendations for raptor surveys and conservation measures in the Guidelines to ensure that proposed projects will avoid adverse impacts to raptors. Locations of existing raptor nests should be identified prior to the initiation of project activities. We recommend that appropriate spatial buffers and timing limits be applied to your project for raptors during crucial breeding and nesting periods relative to raptor nest sites or territories per our Guidelines. Raptors may initiate nesting as early as December for certain species. Nesting and fledging can continue through August and for some species the young may not fledge from nests until September.



United States Department of the Interior

FISH AND WILDLIFE SERVICE
Washington D.C. 20240



DIRECTOR'S ORDER NO.: 225

Subject: Incidental Take of Migratory Birds

Sec. 1 What is the purpose of this Order? The U.S. Fish and Wildlife Service (Service) interprets the Migratory Bird Treaty Act (MBTA) to prohibit incidental take of migratory birds and will enforce the statute accordingly. This Order provides background and guidance to Service employees, including expectations for conducting Service activities, providing technical assistance, and prioritization of our enforcement activities.

Sec. 2 What is the legal authority for this Order? The legal authority for this Order is the MBTA (16 U.S.C. 703-712).

Sec. 3 What terms do you need to know to understand this Order?

- a. **Migratory bird** in 50 CFR 10.12 means "any bird, whatever its origin and whether or not raised in captivity, which belongs to a species listed in 50 CFR 10.13, or which is a mutation or a hybrid of any such species, including any part, nest, or egg of any such bird, or any product, whether or not manufactured, which consists, or is composed in whole or part, of any such bird or any part, nest, or egg thereof." The list of protected birds is maintained in regulation at 50 CFR 10.13 and includes over 1,000 species. Migratory birds are protected based on whether their species, family, or taxonomic group is covered under at least one of the four bilateral migratory bird treaties. Birds are protected even if they do not migrate, no matter their origin, and whether or not they are raised in captivity (50 CFR 10.12).
- b. **Incidental take** means the taking or killing of migratory birds that results from, but is not the purpose of, an activity.¹ Our assessment of whether an activity violates the MBTA will take into account case law, including the case law applicable in particular jurisdictions.
- c. **Beneficial practice** means an action implemented in an effort to avoid and minimize the incidental take of migratory birds. We also refer to beneficial practices as best management practices, conservation measures, best practices, mitigation measures, etc.

¹ Note that "take," and thus incidental take, under the Endangered Species Act (ESA) differs in scope from "take" under the MBTA. Compare 16 U.S.C. 1532(19) and 50 CFR 17.3 with 16 U.S.C. 703(a) and 50 CFR 10.12.

Sec. 4 What is the background for this Order?

- a. A wide range of activities can result in the incidental take of migratory birds, including activities conducted by public- and private-sector entities and the general public. Most individuals and organizations have an interest in, and in the case of Federal entities, a responsibility for, protecting migratory birds.
- b. This Order confirms that the Service has reestablished its longstanding policy and practice of enforcing the MBTA pursuant to its interpretation of the Act as prohibiting the incidental take of birds federally protected on the List of Migratory Birds (50 CFR 10.13). With the October 4, 2021 rulemaking (86 FR 54642), the Service revoked the interpretation codified by the January 7, 2021 rule (86 FR 1134), which had briefly established the opposite interpretation.
- c. With the revocation rule, the Service returns to the interpretation of the MBTA implemented for the previous several decades by the Service, the Department of the Interior, and the Department of Justice. This Order clarifies how we will prioritize program and law enforcement resources consistent with that interpretation upon the effective date of that rule, which is December 3, 2021.

Sec. 5 What is the policy on enforcement of incidental take of migratory birds?

The Service recognizes that a wide range of activities may result in incidental take of migratory birds. Pursuing enforcement for all these activities would not be an effective or judicious use of our law enforcement resources. For that reason, the Service will focus our enforcement efforts on specific types of activities that both foreseeably cause incidental take and where the proponent fails to implement known beneficial practices to avoid or minimize incidental take. Our intention through this policy is to apply a transparent and consistent approach to managing and prioritizing our enforcement of incidental take, taking into account the case law applicable in a given jurisdiction and the facts and circumstances of each case.

- a. The following types of conduct are not a priority for enforcement:
 - (1) A member of the general public conducting otherwise legal activities that incidentally take migratory birds;
 - (2) A Federal agency conducting activities in accordance with a signed memorandum of understanding with the Service developed under Executive Order 13186 for the conservation of migratory birds; or
 - (3) A public- or private-sector entity conducting activities in accordance with applicable beneficial practices for avoiding and minimizing incidental take.
- b. The Service prioritizes the following types of conduct for enforcement:
 - (1) Incidental take that is the result of an otherwise illegal activity; or
 - (2) Incidental take that:
 - (i) results from activities by a public- or private-sector entity that are otherwise legal;
 - (ii) is foreseeable; and

(iii) occurs where known general or activity-specific beneficial practices were not implemented.

- c. The Migratory Bird Program maintains a comprehensive website of beneficial practices, conservation measures, and decision support tools.

Sec. 6 What is the policy on Service activities that may result in incidental take of migratory birds?

- a. Service personnel must review their activities to determine if incidental take is likely. Common actions that may result in incidental take of migratory birds include, but are not limited to, infrastructure construction, operation, and maintenance; vegetation clearing and management; controlled burns; and projects meant to eradicate invasive species.
- b. If an activity will foreseeably result in incidental take of migratory birds, Service personnel must develop and implement beneficial practices to avoid or minimize impacts to migratory birds.
- c. Service personnel should ensure their activities minimize negative effects to migratory bird habitats to promote the conservation of migratory bird populations.
- d. Service personnel may consult with the Regional Migratory Bird Program to review actions for potential effects to migratory birds and their habitats and provide technical assistance on beneficial practices intended to avoid or minimize those effects.

Sec. 7 Where can Service employees find information on beneficial practices to reduce impacts to migratory birds? The Migratory Bird Program maintains a comprehensive website of beneficial practices, conservation measures, and decision support tools. For further assistance, contact Migratory Bird Program representatives.

Sec. 8 What is the status of other guidance relevant to this Order?

- a. This Order revokes and replaces the Director's memorandum entitled "Guidance on the Recent M-Opinion Affecting the Migratory Bird Treaty Act," April 11, 2018.
- b. Solicitor Opinion M-37041, Incidental Take Prohibited Under the Migratory Bird Treaty Act (January 10, 2017), remains suspended and temporarily withdrawn as of February 6, 2017.
- c. Solicitor Opinion M-37050, The Migratory Bird Treaty Act Does Not Prohibit Incidental Take (December 22, 2017), was permanently withdrawn on March 8, 2021.

Sec. 9 When is this Order effective? This Order goes into effect on December 3, 2021. It remains in effect until we incorporate our interpretation that the MBTA prohibits incidental take into the Code of Federal Regulations (CFR), incorporate it into the U.S.

Fish and Wildlife Service Manual, or until we extend, amend, supersede, or revoke it, whichever comes first. If we do not take any of these actions, the provisions of this Order will terminate 18 months from the date it was signed.

Sec. 10 Application. This Order is intended only to improve the internal management of the U.S. Fish and Wildlife Service and does not create any right or benefit, substantive or procedural, separately enforceable at law or equity by a party against the United States, its agencies or instrumentalities, its officers or employees, or any other person.

/sgd/ Martha Williams
PRINCIPAL DEPUTY DIRECTOR,
Exercising the Delegated Authority of the Director,
U.S. Fish and Wildlife Service

Date: October 5, 2021



United States Department of the Interior

FISH AND WILDLIFE SERVICE
334 Parsley Boulevard
Cheyenne, Wyoming 82007



In Reply Refer to:

January 17, 2023

Memorandum

To: Assistant Regional Director, U.S. Fish and Wildlife Service, Ecological Services, Lakewood, Colorado

From: *for* Field Supervisor, U.S. Fish and Wildlife Service, Wyoming Field Office, Cheyenne, Wyoming **NATHAN DARNALL**
Digitally signed by
NATHAN DARNALL
Date: 2023.01.17 14:40:48
+07'00'

Subject: Standing Analysis for Effects to Whitebark Pine (*Pinus albicaulis*) from Low Effect Projects and Whitebark Pine Restoration and Recovery Activities within Montana and Wyoming

On December 15, 2022, the U.S. Fish and Wildlife Service (Service) published a final rule to list the whitebark pine (*Pinus albicaulis*) as threatened under the Endangered Species Act of 1973, as amended (Act; 16 U.S.C. 1531 *et seq.*) (87 FR 76882). The attached Standing Analysis was developed to expedite the consultation process for ongoing maintenance and management actions, new development or construction projects that will damage or kill small numbers of live whitebark pine, and for activities that are beneficial for the restoration or recovery of whitebark pine within Montana and Wyoming. The Standing Analysis considers the range-wide status of the species, the status of whitebark pine within Montana and Wyoming, including threats and the impact of ongoing activities and conservation efforts. The Standing Analysis evaluates these factors and the effects to whitebark pine from recovery activities and other actions considered to have low effects, along with cumulative effects. Based on the Standing Analysis, we developed a determination key to be used in the Service's online Information for Planning and Consultation (IPaC) system.

Federal agencies or their designated representatives may use the determination key in IPaC for consultation. Information submitted online (e.g., project description and location, responses to questions about the project) is evaluated by a determination key in IPaC to ensure that projects fall within the scope of what is analyzed in the Standing Analysis. The Standing Analysis provides the basis for Service concurrence with "may affect but not likely to adversely affect" determinations. The Standing Analysis documents the Service's analysis for a wide variety of small effect actions and activities, and the Standing Analysis can be readily updated with new information.

The determination key in IPaC will be used to evaluate potential effects to whitebark pine from individual projects. Based on the information provided in IPaC, the determination key may confirm that a project either (1) is not anticipated to have any effect on the whitebark pine, or (2) "may affect but is not likely to adversely affect" the whitebark pine. Projects falling into these categories will receive a response either acknowledging the "no effect" determination or

EXECUTIVE SUMMARY

On December 15, 2022, the U.S. Fish and Wildlife Service (Service) published the final rule to list the whitebark pine (WBP) (*Pinus albicaulis*) as a threatened species (87 FR 76882) under the Endangered Species Act of 1973, as amended (Act; 16 U.S.C. 1531 et seq.). The Service also published a final 4(d) rule for WBP that identified actions necessary for the conservation and recovery of the species and included prohibited acts as well as a limited number of exceptions to the prohibited acts (87 FR 76882). Previously, on December 2, 2020, the Service published a proposed rule to list the WBP as threatened with a proposed 4(d) rule under the Act (85 FR 77408). No critical habitat was proposed for WBP. Section 4(d) rules cannot and do not absolve federal agencies of their consultation requirements under section 7 of the Act.

This Standing Analysis provides a basis for section 7 consultation for activities that are not prohibited by the 4(d) rule (see Appendix A for more information on the 4(d) rule). The analysis in this Standing Analysis (SA) evaluates effects to WBP from a variety of actions across Montana and Wyoming, including ongoing maintenance and management actions, new development or construction projects that will damage or remove no more than 125 total WBP trees (seedlings, saplings, and mature trees combined), livestock grazing, right-of-way maintenance, and activities that are beneficial for the restoration or recovery of WBP.

Specifically, activities considered in the framework include:

- a. Livestock management and range improvements: livestock management and range infrastructure improvements (e.g., grazing, gathering and moving, fencing, stock ponds and tanks, and spring development);
- b. Infrastructure actions: infrastructure maintenance, upgrades, and replacement activities for existing pipelines, communication towers, utility lines, renewable energy facilities, trails, and highway infrastructure (e.g., to roads, bridges, culverts, bike and pedestrian facilities, fencing, lighting, and all other distinct aspects of a highway project); construction of new pipelines, communication towers, utility lines, renewable energy projects, and highway infrastructure;
- c. Mineral and conventional oil and gas exploration and development: maintenance of existing locatable and leasable mining and conventional oil and gas projects; new development of existing mineral and conventional oil and gas leases; and new development of new mineral and conventional oil and gas leases;
- d. Vegetation management actions: vegetation (forest) management activities that take into account age class prescriptions, genetic variability within and among WBP populations, and activities that may impact the adaptive potential and the forest trajectories of WBP (salvage harvests and pest control that remove dead and diseased trees and encourage natural WBP recruitment and are not in existing WBP restoration areas); timber harvest projects, hazardous fuel removal (in Wildland Urban Interface (WUI) areas), and precommercial thinning and group selection projects;
- e. Recreation activities: maintenance of existing trail systems (hiking and biking specifically); maintenance of existing recreational development projects (e.g., ski resorts and campgrounds), and other recreational activities (e.g., off-highway vehicles (OHV) and over-snow vehicles (OSV) use); upgrades, replacement, expansion, or new construction outside the existing disturbance footprint of existing recreation projects, and outfitter and guide permit programs;

concurring with the “may affect but is not likely to adversely affect” determination. Projects that fall outside the bounds of the Standing Analysis and projects that “may affect and are likely to adversely affect” whitebark pine, even if they are addressed in the Standing Analysis, are not part of the online determination key in IPaC at this time.

No Effect (NE) Determination

Based on the Standing Analysis, projects within the area of influence (species range) but for which whitebark pine are not present and projects involving only dead trees (no live seedling, sampling, or mature trees) will have no effect (NE) on whitebark pine. Concurrence from the Service is not required for NE determinations; however, IPaC will deliver a letter documenting the outcome of the determination key.

May Affect, Not Likely to Adversely Affect (NLAA) Determination

The Standing Analysis concludes that projects occurring more than 10 meters (33 feet) from any live whitebark pine trees (seedling, sapling, and mature trees) will result in insignificant, discountable, or wholly beneficial effects to the whitebark pine, resulting in a “may affect, not likely to adversely affect” (NLAA) determination (more specifically described in the Standing Analysis). We also anticipate that agencies will implement the appropriate conservation measures from the Standing Analysis and adhere to the most recent best management practices to minimize impacts to whitebark pine.

It is the federal agency’s responsibility to make a final effect determination for potential impacts resulting from actions they conduct or permit and to confirm that the project is consistent with the determination key’s questionnaire and output. This letter only addresses whitebark pine. If other listed species or critical habitat occur within a project area or may be affected by a project, a separate consultation with the Service may be necessary.

Questions regarding this memo or responsibilities under the Act should be directed to the Wyoming Ecological Services Field Office at the letterhead address, by email at WyomingES@fws.gov, or by phone at (307) 772-2374.

may remove no more than 125 trees, thus providing an additional buffer. However, we will continue to evaluate development projects that remove more than 125 WBP trees separately (outside of this SA), even if the aggregate number of trees removed per year is less than 12,500 (of which, 5,000 are assumed to be rust-resistant). We anticipate the recovery efforts (*e.g.*, planting rust-resistant trees) will either remain the same or are likely to increase after the species has been listed under the Act; however, we will continue to use the approach described above and its thresholds rather than increasing the number of projects and trees. We will re-evaluate this SA at least annually and will reconsider its application, use, thresholds, and efficacy at a minimum of five years after implementation.

2.f. Conservation Measures

To fully understand the extent of the effect that individual project activities analyzed by the SA will have on WBP trees (seedlings, saplings, and mature trees), and to avoid and minimize these impacts, the SA provides a detailed list of successfully-implemented conservation measures from which project applicants can choose. We consider the damage of a WBP to include, but is not limited to, soil tilling, disking, plowing, excavating, raking, sod rolling, soil compaction, soil disturbance, weed management, revegetation, crushing, bumping, and scraping WBP, root damage, mycorrhizal damage, nicks and opening wounds on WBP bark, and pruning.

The following conservation measures are considered part of the actions under the SA. The commitments and implementation of the following conservation measures and exploration of additional opportunities to reduce impacts made by the federal action agencies will reduce adverse effects of the proposed actions to the WBP. These conservation measures will become commitments by federal action agencies where appropriate and practicable. Many of these conservation measures are to be applied throughout the action area, though others specify the location or distance from WBP trees for application. Not all conservation measures are applicable or reasonable for all actions that are covered under this SA. The Determination Key includes a section where project applicants must select which of the following conservation measures they plan to implement as part of their action, which will be repeated back to the applicant in our IPaC generated response letter or memo:

General

- CM 1. Conduct pre-project surveys to identify WBP individuals of all age classes. If not feasible, conduct surveys using appropriate agency protocols to estimate the number of WBP individuals of all age classes.
- CM 2. When marking is appropriate, all mature WBP trees or clusters of other age class trees will be marked in a manner that does not cause damage to the tree or introduce disease.
- CM 3. Damaging or killing a plus, elite, or phenotypically resistant tree will only occur in situations where human health and safety are at risk or when restoration actions such as pruning are occurring.

3. Status of the Species

This SA provides a general background on the status of the species and its habitat, relying on the Service's 2021 SSA (USFWS 2021, entire). No critical habitat has been designated for this species. A detailed status of the WBP's biology, range, habitat, needs, stressors, and conservation can be found in Appendix C.

The WBP is a five-needle conifer species placed in the subgenus *Strobis*, which also includes other five-needle white pines. Recent phylogenetic studies (Liston *et al.* 1999; Syring *et al.* 2005, 2007; as cited in Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2010) showed no difference in monophyly (ancestry) between subsection *Cembrae* and subsection *Strobi* and merged them to form subsection *Strobis*. No taxonomic subspecies or varieties of WBP are recognized (COSEWIC 2010). Based on this taxonomic classification information, we recognize WBP as a valid species (USFWS 2021).

There are four stages in the life cycle of the WBP: seed, seedling, sapling and mature trees, also referred to as reproductive adults. Seeds are produced in female cones and once on the ground may take two years or more, up to 11 years in some cases, to germinate. Germinated seeds become seedlings that are between 3 to 4 inches tall (8 and 10 centimeters) with a taproot that can measure between 5 to 7 inches (13 to 18 centimeters), with 7 to 9 cotyledons, also known as the embryonic first leaves, as documented by (Arno and Hoff 1989). WBP seedlings may persist for multiple years, depending on growing conditions, until reaching the sapling stage of the life cycle. WBP saplings persist for few to many years, depending on growing conditions, until they produce male and female cones. Mature reproductive WBPs contain both female and male cones, which is known as monoecious reproduction, and can survive on the landscape for hundreds of years. This slow-growing long-lived tree with a life span between 500 years and 1,000 years (Arno and Hoff 1989; Perkins and Swetnam 1996), provided it is located in an area with lower competition, such as a more open canopy with low litter depth and high rock cover (Maloney 2014). Therefore, in addition to the four general needs for all life stages, mature WBP trees require a more open canopy, dispersal of seeds by Clark's nutcracker, two summers of suitable temperatures and precipitation for pollinated cones to mature, as well as levels of nitrogen and phosphorus that are adequate to restore values after being depleted in masting year (USFWS 2021).

The WBP is a five-needle pine that lives in windy, cold, high-elevation or high-latitude environments across the western United States and southern Canada. The WBP pine has a broad range both latitudinally, occurring from a southern extent of approximately 36° north in California to 55° north latitude in British Columbia, Canada, and longitudinally, occurring from approximately 128° in British Columbia, Canada to an eastern extent of 108° west in Wyoming. It also occurs in scattered areas of the warm and dry Great Basin. As a result, many stands are geographically isolated as documented by (Arno and Hoff 1989).

Most current management and research focus on producing and planting white pines (including WBP) with genetic resistance to white pine blister rust, but also include natural regeneration (e.g., those areas identified in Appendix B, Tables A, B, and C) and silvicultural treatments, such as appropriate site selection and preparation, pruning, and thinning (Zeglen *et al.* 2010).

5.d. Forest (Vegetation) Management Actions

Forest (vegetation) management includes a variety of methods and techniques used to manage healthy forests, and known previous projects that fall within this action type are summarized in Table D of Appendix C. These types of forest management activities include timber harvest (using chainsaws and using machinery which may create skid trails) and management/hazardous fuels reduction (using chainsaws and using machinery which may create skid trails, to remove dead and dying trees and understory vegetation that may carry wildfire), salvage harvest (removing dead trees either by hand or using machinery which may create skid trails), pest control (use of Verbenone or Carbaryl insecticide), precommercial thinning (thinning trees that are too small for a commercial timber harvest), silviculture stand improvement projects (using a planned set of treatments such as thinning, harvesting, planting, pruning, prescribed burning, and site preparation designed to change the current stand structure and composition to one that meets a management goal), and silvicultural reforestation activities (planning for natural regeneration or tree planting).

Forest management related road construction, maintenance, and use may also be part of vegetation management projects. Harvest of WBP has not been well tracked as records often group it with other species and incorrectly identify it as another species. Silviculture approaches create a system that excludes regeneration opportunities and increases competition by planting faster-growing species, and consequently, stands that contain WBP prior to harvest are not routinely replanted with WBP.

Projects that implement resetting the successional stage of the forest stands need to be carefully thought out and planned to increase WBP recruitment. Campbell and Antos (2003) noted that successional patterns in WBP forests are more complex than others have reported, finding that subalpine fir readily established after fire in their British Columbia study areas, and although subalpine fir density was increasing in older WBP stands with relatively open canopies, they estimated that succession to subalpine fir would take more than 500 years. Campbell and Antos (2003) reported that WBP in their study area was stress-tolerant (able to persist under conditions that restrict production), was capable of surviving long periods of suppressed growth, and was able to release upon reaching the main canopy after more than 150 years of low growth rates. The results of these studies indicate that the loss of WBP due to succession to subalpine fir and Engelmann spruce in some areas may be an extremely slow process and that WBP may be more shade-tolerant and resilient to suppression than previously suggested. Further, thinning and timber harvest projects intended to improve WBP recruitment may increase WBP susceptibility to mountain pine beetle infestation, if the beetles do not have their preferred food sources during outbreak years. The densification of and succession of subalpine fir and Engelmann spruce co-occurred with WBP mortality caused by bark beetle outbreaks and/or blister rust; therefore, disentangling the effects of blister rust- and bark beetle-mortality on succession from the effects of fire suppression in these studies is difficult (Hartwell *et al.* 1997; Arno *et al.* 1993 in Keane *et al.* 1994; Flanagan *et al.* 1998).

Projects including those in WUI, salvage harvests, and pest control efforts remove dead and diseased trees, and may encourage natural WBP recruitment. In large acreages of dead trees, salvage harvest and firewood cutting projects can be designed to avoid damaging or killing live

Appendix C. Status of the Species

This appendix provides a more detailed status of the species than what is included in the body of the SA. To understand the current status of the species, we must identify specific life stages: seedling, sapling, and mature WBP are described under the following definitions of their life stages. First year seedlings are those recently germinated with no mature foliage and have not experienced a winter. The *seedling stage* of WBP is detectable when a germinated seeds reach growth between 8 and 10 cm (3 to 4 in.) tall with a 13 to 18 cm (5 to 7 in.) taproot, and 7 to 9 cotyledons (embryonic first leaves) (Arno and Hoff 1990). The WBP seedling stage is generally when the trees are between 1 and 29 years of age and are up to 1.37 m (4.5 ft), which is the height assessed at diameter at breast height (dbh) (Tomback and Pansing 2018). *Saplings* are non-reproductive trees greater than 1.37 m (4.5 ft) in height; for WBP. The average age of reproductive maturity (*mature WBP*) is 29 to 40 years of age (Tomback and Pansing 2018). Some WBP individuals are capable of producing limited amounts of seed cones at 20–30 years of age, although large cone crops usually are not produced until 60–80 years (Krugman and Jenkinson 1974, as cited in McCaughey and Tomback 2001), with average earliest first cone production at 40 years (Tomback and Pansing 2018). Therefore, the generation time of WBP is approximately 40 to 60 years (Tomback and Pansing 2018; COSEWIC 2010). Size class data should not be used as a surrogate for determining the age class of a WBP tree. Larson and Kipfmüller (2012) found small subalpine fir trees occurring below the WBP trees that visually appeared to be young saplings were more than 100 years of age.

1. Taxonomy

The WBP is a five-needle conifer species placed in the subgenus *Strobus*, which also includes other five-needle white pines. This subgenus is further divided into two sections (*Strobus* and *Parrya*), and under section *Strobus*, into two subsections (*Cembrae* and *Strobi*). *Strobus* sp have five-needled fascicles, wingless seeds, and cones that remain closed at maturity (Lanner, 1990). Stone pines are morphologically defined by wingless seeds and cones that remain closed at maturity, retaining their seeds within (Lanner, 1990). The traditional taxonomic classifications placed WBP in the subsection *Cembrae* with four other Eurasian stone pines (Critchfield and Little 1966; Lanner 1990). However, recent phylogenetic studies (Liston *et al.* 1999; Syring *et al.* 2005, 2007; as cited in Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2010) showed no difference in monophyly (ancestry) between subsection *Cembrae* and subsection *Strobi* and merged them to form subsection *Strobus*. No taxonomic subspecies or varieties of WBP are recognized (COSEWIC 2010). Based on this taxonomic classification information, we recognize WBP as a valid species.

2. Life History

There are four stages in the life cycle of the WBP: seed, seedling, sapling, and mature trees (*i.e.*, reproductive mature trees). Seeds are produced in female cones and may take 2 years or more (up to 11 years) to germinate. Germinated seeds become seedlings that are between 8 and 10 centimeters (cm) (3 to 4 inches) (in.) tall with a 13 to 18 cm (5 to 7 in.) taproot with 7 to 9 cotyledons (embryonic first leaves) (Arno and Hoff 1990). WBP seedlings are generally

between one and 29 years of age and, on average, are 1.37 m (4.5 ft), which is the height assessed at dbh (Tomback and Pansing 2018). WBP seedlings have highly variable survival rates; seedlings originating from nutcracker caches ranged from 56 percent survival over the first year to 25 percent survival by the fourth year (Tomback 1982). Seedlings of WBP may persist for multiple years, depending on growing conditions, until reaching the sapling stage of the life cycle. Saplings are non-reproductive trees greater than 1.37 m (4.5 ft) in height; for WBP, the average age of reproductive maturity is 29 to 40 years of age (Tomback and Pansing 2018). Saplings of WBP persist for few to many years, depending on growing conditions, until they produce male and female cones and are considered reproductive at approximately 60 years of age. Some WBP individuals are capable of producing limited amounts of seed cones at 20 to 30 years of age, although large cone crops usually are not produced until 60 to 80 years (Krugman and Jenkinson 1974, as cited in McCaughey and Tomback 2001), with average earliest first cone production at 40 years (Tomback and Pansing 2018). Therefore, the generation time of WBP is approximately 40 to 60 years (Tomback and Pansing 2018; COSEWIC 2010). Mature WBP trees require two summers of suitable temperatures and precipitation for fertilized cones to mature (Rapp *et al.* 2013). Years with high seed production (mast years) typically occur once every three to five years; however, that time interval can vary by geographic location and health condition of the stand (McCaughey and Tomback 2001). After such a masting year, each individual WBP is depleted of nitrogen and phosphorus and so those nutrients must be replaced during the three to five years between masting events (Sala *et al.* 2012). Mature reproductive WBP trees contain both female and male cones (*i.e.*, monoecious reproduction), and can survive on the landscape for hundreds of years.

The WBP is the only stone pine (so-called for their stone-like seeds) in North America of the five species worldwide (McCaughey and Schmidt 2001). Characteristics of stone pines include five needles per cluster, indehiscent seed cones (scales remain essentially closed at maturity) that stay on the tree, and wingless seeds that remain fixed to the cone and cannot be dislodged by the wind. Because WBP seeds cannot be wind disseminated, primary seed dispersal occurs almost exclusively by Clark's nutcrackers in the avian family Corvidae (whose members include ravens, crows, and jays) (Lanner 1996; Schwandt 2006). Consequently, Clark's nutcrackers facilitate WBP regeneration and influence its distribution and population structure through their seed caching activities (Tomback *et al.* 1990).

The WBP may occur as a climax species, early successional species, or seral (mid-successional stage) codominant associated with other tree species. Although it occasionally occurs in pure or nearly pure stands at high elevations, it more typically occurs in stands of mixed species in a variety of forest community types. WBP is typically 5 to 20 m (16 to 66 ft) tall with a rounded or irregularly spreading crown shape. On higher density conifer sites, WBP tends to grow as tall, single-stemmed trees, whereas on open, more exposed sites, it tends to have multiple stems (McCaughey and Tomback 2001). Above the tree line, it grows in a krummholz form (stunted, shrub-like growth) (Arno and Hoff 1989). Production of male and female cones in mature trees will begin sometime from June to September depending on environment (McCaughey and Tomback 2001; Sala *et al.* 2012). Female cones take 2 years to fully develop (Weaver 2001). Its characteristic dark brown to purple seed cones are 5 to 8 cm (2 to 3 in.) long and grow in clusters of 2 to 4 cones at the outer ends of upper branches (Hosie 1969).

Ensuring future generations of WBP are genetically resistant to white pine blister rust is the most critical action for achieving long-term recovery of this species (Mahalovich and Dickerson 2004; Perkins *et al.* 2016). Genetic management of white pine blister rust is actively conducted for WBP, including the USFS white pine blister rust resistance screening programs (Mahalovich 2016; Snieszko 2016). Seeds and pollen sourced from plus trees or elite trees are used for screening and selective breeding for white pine blister rust resistance (not immunity), molecular genetics studies, assessing levels of inbreeding, growing compatible rootstock for grafting in seed orchards, clone banking and gene conservation, and identifying genetic macro-refugia (Mahalovich 2016; Perkins *et al.* 2016; Snieszko 2016).

Eventually, the long-term goal is to establish WBP seed orchards in situ across the spectrum of WBP habitat to provide reliable and accessible sources of genetically resistant seed (Mahalovich 2017). Scions (*i.e.*, living branches) taken from trees with proven genetic resistance to white pine blister rust are grafted onto established root stocks, enabling them to develop the capability to produce cones much sooner than the time required for out planted seedlings to reach reproductive maturity (approximately 60 years).

Seeds from cone collections in the northwest (*i.e.*, Washington, Oregon) are now stored at the United States Department of Agriculture (USDA) National Center for Genetic Resources Preservation in Fort Collins, Colorado for long-term ex situ gene conservation (Snieszko and Kegley 2017). Seven separate white pine blister rust screening trials are occurring at the USFS Coeur d'Alene Nursery in Idaho using over 100,000 seedlings (Mahalovich 2016, 2017).

4.c. Fuel Reduction Treatment

Silvicultural practices, such as thinning, are frequently employed to treat existing stands of WBP to modify surface and ladder fuels and improve their chances of surviving fire. Table D of Appendix C describes the silvicultural and restoration activities in WBP habitat within Montana between 2009 and 2021 and Wyoming between 1991 and 2020. Most thinning treatments are designed to mimic non-lethal mixed-severity fire (Keane and Arno 2001), reduce or eliminate competition from other conifer species such as subalpine fir (*Abies lasiocarpa*), and to increase regeneration space for potentially rust-resistant seedlings. Approaches include creating openings wherein all trees except live WBPs are cut within a 1- to 5-ac opening to provide open growing space for WBP regeneration and existing WBP trees (Keane and Arno 2001; Keane and Parsons 2010); thinning of all non-WBP trees below a certain diameter (Chew 1990); and fuel enhancement treatments where other competing trees are directionally felled to modify fire behavior and reduce fire intensity (Keane and Arno 2001; Keane and Parsons 2010). Reducing tree density within WBP stands may result in increased vigor (*i.e.*, growth rate) of remaining sapling to mature-class trees (Keane *et al.* 2007; Retzlaff *et al.* 2018); however, counterintuitively, increased WBP vigor may not impart increased resistance to mountain pine beetle, as some evidence suggests that mountain pine beetles select faster growing trees for attack (Six *et al.* 2021). In addition to or in place of treating fuels within WBP stands, managers should consider conducting fuel reduction treatments in non-WBP stands adjacent to WBP, thereby reducing the intensity of fire as it moves from the adjacent stand into the WBP stand.

WBP both as a stressor that can cause mortality of all life stages of WBP and as a mechanism that may affect forest succession (Arno 2001; Shoal *et al.* 2008; Keane and Parsons 2010). Although WBP has been described as fire-adapted, there is uncertainty surrounding the specifics of these adaptations, including the species' ability to survive fires of differing intensity, the role of low-severity fire, and how fire suppression interacts with fire return intervals to affect forest succession across the range of WBP.

Fire regimes in WBP systems are often characterized as being of mixed severity (Arno *et al.* 2000; Arno 2001, Campbell and Antos 2003; Larson *et al.* 2009). However, some WBP systems are dominated by high-severity fire events (Romme 1982; Campbell and Antos 2003). Low-severity surface fires may also occur in WBP stands, particularly at higher elevations (Barrett 1994). Clark's nutcracker ecology provides further insight into the typical fire regime in WBP ecosystems. The Clark's nutcracker serves as the main dispersal agent for WBP (Tomback *et al.* 2001). Eighty-five percent of the WBP seeds cached are above ground in the trunks of live trees. In most cases Clark's nutcracker avoids caching seeds in forest openings (Brodin and Clark 2007; Lorenz 2011; Lorenz *et al.* 2012). Clark's nutcrackers have been found dispersing seeds farther than the wind-dispersed seeds of other conifers, allowing for the establishment of WBP seedlings in the interior of large patches of high severity fire effects and over broad geographic areas (McCaughy *et al.* 1985; Tomback *et al.* 1990, 1993 in Keane and Parsons 2010). To promote a greater than 75 percent probability of Clark's nutcracker occurrence at a site containing WBP, the landscape composition must contain a minimum 12,500 to 25,000 ha cone bearing WBP within a 32.6-km radius (Schaming and Sutherland 2020). Clark's nutcrackers feed equally on Douglas-fir seeds and WBP seeds, so the optimal habitat mosaic includes moderate levels of Douglas-fir habitat (Schaming 2016).

Although some experts have suggested that WBP is phenotypically adapted to survive low-intensity fire, Stevens *et al.* (2020) found that WBP had relatively thin bark compared to other conifer species and, based on a systematic ranking of numerous traits associated with fire resistance in western conifers, WBP was found to have one of the lowest fire resistance scores of the 29 conifers examined in the study. Others have also observed that WBP trees can be sensitive to bole (main stem of the tree) scorching, resulting in cambium injury or death, even from low-intensity fire (Hood *et al.* 2008). Keane *et al.* (2020) noted several recent reports of prescribed fire and low-intensity fire killing WBP trees, despite pre-fire site preparation activities implemented to reduce or modify surface and ladder fuels and protect the residual WBP trees. Keane and Parsons (2010) studied the effects of seven different fuel treatment combinations on WBP at five treatment sites in Montana and Idaho and found that WBP mortality from low-intensity fire was comparable to subalpine fir under all treatment combinations. As a result, empirical evidence shows that low-intensity fire in WBP can result in higher-severity fire effects. In summary, although it is clear that WBP individuals are capable of surviving some low-intensity fire, based on the presence of multiple fire scars in some areas, the biotic and abiotic (*i.e.*, terrain, weather, and fuel) conditions under which the species is most likely to survive such fires remain largely unknown.

Determining if periodic fire is necessary to maintain ecosystem integrity in WBP systems may be as important as understanding the conditions under which WBP trees are most likely to survive fire. Experts have suggested that, without periodic low-severity fire in some subalpine forests

where WBP co-occurs with subalpine fir and Engelmann spruce, successional pathways can lead to climax communities dominated by these shade-tolerant conifers and the loss of WBP (Arno 1980; Arno 2001; Keane *et al.* 2017; Keane and Parsons 2010; Flanagan *et al.* 1998). It has further been suggested that, in these WBP systems, fire suppression policies over the past 90 years have resulted in WBP declines due to succession to subalpine fir and Engelmann spruce (Arno 1980; Arno 2001; Keane *et al.* 2017; Keane and Parsons 2010; Flanagan *et al.* 1998). This is supported by the presence of multiple fire scars in WBP trees at some locations, which shows they are capable of surviving repeated low-intensity fires and maintaining dominance or co-dominance in stands for long-periods of time when these fires are occurring periodically (Morgan and Bunting 1990, Barrett 1994). Additional support for the successional theory is based on documented densification of subalpine fir and Engelmann spruce in stands where WBP was once prevalent (Hartwell *et al.* 1997; Arno *et al.* 1993 in Keane *et al.* 1994; Flanagan *et al.* 1998). However, in these studies, the authors noted that the densification of and succession to subalpine fir and Engelmann spruce co-occurred with WBP mortality caused by bark beetle outbreaks and/or blister rust; therefore, disentangling the effects of blister rust- and bark beetle-mortality on succession from the effects of fire suppression in these studies is difficult.

The idea that fire suppression in some whitebark systems has resulted in densification and loss of WBP has been a predominant theory in the WBP literature (Arno 1980; Arno 2001; Keane *et al.* 2017; Keane and Parsons 2010; Flanagan *et al.* 1998). However, some have recently called into question the idea that fire suppression has led directly to forest succession and the loss of WBP. For example, Larson and Kipfmüller (2012) suggested there is uncertainty in the effects of fire suppression on WBP and a relative lack of data supporting the hypothesis. Larson and Kipfmüller (2012) noted that age structure data in their study showed that many of the small subalpine fir trees occurring below the WBP, trees that visually appeared to be young saplings, were more than 100 years of age, suggesting that size class data should not be used as a surrogate for tree age or to determine the rate of succession. Campbell and Antos (2003) also noted that successional patterns in WBP forests are more complex than others have reported, finding that subalpine fir readily established after fire in their British Columbia study areas, and although subalpine fir density was increasing in older WBP stands with relatively open canopies, they estimated that succession to subalpine fir would take more than 500 years. Campbell and Antos (2003) reported that WBP in their study area was stress-tolerant (able to persist under conditions that restrict production), was capable of surviving long periods of suppressed growth, and was able to release upon reaching the main canopy after more than 150 years of low growth rates. The results of these studies indicate that the loss of WBP due to succession to subalpine fir and Engelmann spruce in some areas may be an extremely slow process and that WBP may be more shade-tolerant and resilient to suppression than previously suggested.

The broad range of fire return intervals in WBP ecosystems further complicates theories that fire suppression has caused succession in WBP systems. Fire history studies in WBP forests have identified fire return intervals ranging from 33 years (Morgan and Bunting 1990) to greater than 400 years (Campbell and Antos 2003). Several authors have noted that mean fire return intervals in subalpine forests that include WBP can be much longer than contemporary fire suppression policies (Dolanc *et al.* 2013; Meyer and North 2019; Sibold *et al.* 2006). Over an 80-year period, Dolanc *et al.* (2013) documented an increase in the number of small diameter trees, including WBP, in subalpine forests of the central Sierra Nevada. However, Dolanc *et al.* (2013)

Beetle activity in the phloem mechanically girdles the host tree, disrupting nutrient and water transport and ultimately killing it. Additionally, mountain pine beetles carry symbiotic blue stain fungi on their mouthparts, which are introduced into the host tree upon feeding. These fungi also inhibit water transport and further assist in killing the host tree (Raffa and Berryman 1987; Keane *et al.* 2012).

Mountain pine beetles are considered an important component of natural forest disturbance regimes (Raffa *et al.* 2008; Bentz *et al.* 2010). At endemic, or more typical levels, mountain pine beetles remove relatively small areas of trees, changing stand structure and species composition in localized areas. However, when conditions are favorable (abundant hosts and favorable climate), mountain pine beetle populations can erupt to epidemic levels and create stand-replacing events that may kill 80 to 95 percent of suitable host trees (Berryman 1986 as cited in Keane *et al.* 2012). Such outbreaks are episodic, can have a magnitude of impact on the structure of western forests greater than wildfire (the other major component of natural forest disturbance), and are often the primary renewal source for mature stands of western pines (Hicke *et al.* 2006; Raffa *et al.* 2008; Six *et al.* 2014). Mountain pine beetle outbreaks typically subside only when suitable host trees have been exhausted or temperatures are sufficiently low to kill larvae and adults (Gibson *et al.* 2008).

The range of the mountain pine beetle completely overlaps with the range of the WBP, and mountain pine beetle epidemics affecting WBP have occurred throughout recorded history (Keane *et al.* 2012). Recent outbreaks occurred in the 1930s, 1940s, and 1970s, and numerous ghost forests of dead WBP still dot the landscape as a result (Arno and Hoff 1989; Perkins and Swetnam, 1996, Ward *et al.* 2006). The most recent mountain pine beetle epidemic began in the late 1990s and continues to be a measurable but much reduced source of mortality for WBP (MacFarlane *et al.* 2013; Mahalovich 2013; Shelly 2014) (Figure A).

contorta var. *murrayana*) and mountain hemlock is absent from the Blue Mountains (Arno and Hoff 1990; McCaughey and Schmidt 2001).

Rangewide, WBP occurs on an estimated 32,616,422 ha (80,596,935 ac) in western North America (Figure 2 of the SA). Roughly 70 percent of the species' range occurs in the United States, with the remaining 30 percent of its range occurring in British Columbia and Alberta, Canada (USFWS 2018). In Canada, the majority of the species' distribution occurs on federal or provincial crown lands (COSEWIC 2010). In the United States, approximately 88 percent of land where the species occurs is federally owned or managed (Figure 2 of the SA). The majority is located on USFS lands (approximately 74 percent, or 17,391,455 ha (42,975,220 ac)). The bulk of the remaining acreage is located on NPS lands (approximately 10 percent, or 2,275,746 ha (5,623,490 ac)). Small amounts of WBP also can be found on BLM lands (approximately 4 percent, or 1,002,152 ha (2,476,371 ac)). The remaining 12 percent of the range is under non-federal ownership, on State, private, and Tribal lands. In the United States, 29 percent of the range is designated as wilderness under the Wilderness Act of 1964 (16 U.S.C. 1131-1136). This designation limits management options and conservation efforts in those areas to some degree.

Populations are typically defined by the potential for genetic exchange among their members, to the exclusion of members of other populations (in the absence of immigration or emigration). For WBP, genetic exchange is limited by the dispersal distance of pollen, which is carried by wind, and the seed caching behavior of Clark's nutcracker (Lorenz *et al.* 2011; Keane *et al.* 2017b). Both pollen dispersal and Clark's nutcracker seed dispersal can occur at a scale of few to many kilometers (km) (e.g., up to 30 km in the case of Clark's nutcracker seed dispersal). To promote a greater than 75 percent probability of occurrence of Clark's nutcracker at a site, recommended management plans that achieves landscape composition of a minimum 12,500-25,000 ha of cone bearing WBP habitat within a 32.6-km radius. The optimal Clark's nutcracker habitat mosaic includes moderate levels of Douglas-fir habitat (Douglas-fir seeds are another important food source for Clark's nutcracker in the GYE) (Schaming 2016 and Schaming and Sutherland 2020). WBP is a long-lived species that exhibits masting, where years of high seed production are synchronized within a population approximately every 3 to 5 years (McCaughy and Tomback 2001). This masting strategy is an adaption to heavy seed predation; during masting years seed consumers are satiated, resulting in excess seeds that escape predation (Lorenz *et al.* 2008). WBP populations need a certain density of reproductive individuals to produce sufficient pollen clouds that facilitate the synchronization of masting, and thus increased probability of regeneration (Rapp *et al.* 2013).

4. Conservation Actions and Restoration Strategies

Most current management and research focus on producing and planting white pines (including WBP) with genetic resistance to white pine blister rust, but also include natural regeneration (e.g., those areas identified in Appendix B, Tables A, B, and C) and silvicultural treatments, such as appropriate site selection and preparation, pruning, and thinning (Zeglen *et al.* 2010). Genetic management of white pine blister rust is actively conducted for several five-needle white pine species breeding programs (Snieszko 2016, Mahalovich 2015, Mahalovich 2010, Shelley 2016) including the USFS resistance screening programs for WBP. High-elevation pines such as WBP also present management challenges to restoration due to remoteness, difficulty of access, a

Considered a keystone, or foundation species in western North America, WBP it increases biodiversity and contributes to critical ecosystem functions (Tomback *et al.* 2001). As a pioneer or early successional species, it may be the first conifer to become established after disturbance, subsequently stabilizing soils and regulating runoff (Tomback *et al.* 2001). At higher elevations, snow drifts around WBP trees, thereby increasing soil moisture, modifying soil temperatures, and holding soil moisture later into the season (Farnes 1990). These higher elevation trees also shade, protect, and slow the progression of snowmelt, essentially reducing spring flooding at lower elevations. The WBP also provides nutritious seeds for a number of birds and mammals (Tomback *et al.* 2001).

3. Population Dynamics, Status and Distribution

The WBP has persisted in high elevation sites in western North America for the past 8,000 years (McCaughey and Schmidt, 2001). WBP has a broad range both latitudinally (occurring from approximately 36 degrees in south California to 55 degrees north latitude in British Columbia, Canada) and longitudinally (occurring from approximately 128 degrees in British Columbia, Canada to 108 degrees east in Wyoming). For the SSA, we developed an updated WBP range map based on the best available occurrence and distribution data (Figure 2 of the SA). This range map is at a coarse scale but encompasses the known distribution of the species' occurrences.

The WBP typically occurs on cold and windy high-elevation or high-latitude sites in western North America, although it also occurs in scattered areas of the warm and dry Great Basin. As a result, many stands are geographically isolated (Arno and Hoff 1989; Keane *et al.* 2010). The distribution of WBP includes coastal and Rocky Mountain ranges that are connected by scattered populations in northeastern Washington and southeastern British Columbia (Arno and Hoff 1990; Keane *et al.* 2010). The coastal distribution of WBP extends from the Bulkley Mountains in northwestern British Columbia to the northeastern Olympic Mountains and Cascade Range of Washington and Oregon, to the Kern River of the Sierra Nevada Range of east-central California (Arno and Hoff 1990). Isolated stands of WBP are known from the Blue and Wallowa Mountains in northeastern Oregon and the subalpine zone of mountains in northeastern California, south-central Oregon, and northern Nevada (Arno and Hoff 1990; Keane *et al.* 2010). The Rocky Mountain distribution of WBP ranges from northern British Columbia and Alberta to Idaho, Montana, Wyoming, and Nevada (Arno and Hoff 1990; Keane *et al.* 2010), with extensive stands occurring in the Yellowstone ecosystem (McCaughey and Schmidt 2001).

In general, the upper elevational limits of WBP decrease with increasing latitude throughout its range (McCaughey and Schmidt 2001). The elevational limit of the species ranges from approximately 900 m (2,950 ft) at its northern limit in British Columbia to 3,660 m (12,000 ft) in the Sierra Nevada (McCaughey and Schmidt 2001). WBP is typically found growing at the subalpine treeline or with other high-mountain conifers just below the treeline and subalpine zone (Arno and Hoff 1990; McCaughey and Schmidt 2001). In the Rocky Mountains, common associated tree species include lodgepole pine (*P. contorta* var. *latifolia*), Engelmann Spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and mountain hemlock (*Tsuga mertensiana*). Common associated tree species are similar in the Sierra Nevada and Blue and Cascade Mountains, except lodgepole pine is present as Sierra-Cascade lodgepole pine (*P.*

WBP, which may be resistant to blister rust. Projects where the removal of surface and ladder fuels through hand cutting, piling of project generated materials, and burning the piles with the purpose of increasing stand resilience to fire may also be beneficial for the recruitment of WBP. Felling trees and creating skid trails for salvage harvests may damage or kill WBP seedlings and saplings and compress the soil and undetected seeds. Implementation of the conservation measures (e.g., CM 1-10, 12-14, and 16-21) in the project design that avoid impacts to WBP seedlings, saplings, and live mature trees, and that minimizes soil disturbance and compaction that may destroy microsites for cached seeds, interrupts drainage, and limits tree rooting will have beneficial long-term impacts to WBP.

Vegetation management includes many project types (e.g., WUI, salvage harvest of dead trees, harvest of Christmas trees, pest control, firewood collection) and sizes (less than 1 acre to thousands of acres). In this SA, we evaluated the effects of smaller forest management projects that damage or kill fewer than 125 live WBP of all age classes. Effects of larger project will be addressed by a standalone consultation or may be covered by a future standing analysis. We have elected to use a limit of 125 WBP of all age classes as a threshold for forest (vegetation) management projects, based on our understanding of the stressors to WBP, the level of ongoing restoration efforts, and our commitment to track and re-evaluate project impacts and restoration efforts for the life of this SA. While forest management projects will result in adverse effects to WBP, these should not result in population level effects for the reasons described above.

5.e. Recreation Development and Activities

The following recreational activities commonly occur in WBP habitat: construction and maintenance of hiking trails and roads (analyzed in the Infrastructure section); motorized use of trails year-round; (snow machines, all-terrain vehicles (ATV), utility task vehicles (UTV), motorcycles, electric bikes, and mountain bikes); operation of facilities (snow making, lift chairs analyzed in the Infrastructure section); firewood consumption; special use permits (hunting, photography); and horseback riding.

There are 91 recreation sites within WBP habitat in the action area, including developed campsites, horse corrals, trail heads, parking areas, toilets, staging areas, scenic overlooks, and primitive campsites. Back country campers and hikers may burn WBP for campfires, cause ground compression, climb on trees, or remove WBP when clearing trails. Motorized recreation activities, hiking, use of pack animals, and construction equipment used for trail maintenance and construction, may cause soil disturbance and compaction, destroy microsites for cached seeds, interrupt drainage, limit tree rooting, and damage seedlings. Over snow vehicles (OSV) could break the tops of trees or could damage branches or seedlings and saplings. We acknowledge that there may be some damage and death to WBP seedlings and saplings from authorized and unauthorized off-road motorized recreation activities which could affect individuals or local areas. Overall, impacts from all recreation activities could affect less than one percent of the species wide range (based on IUCN threats summary for WBP in Canada) (USFWS 2021) and are not considered a significant threat to WBP.

We conclude that, while not all adverse effects can be avoided, the implementation of the conservation measures (e.g., CM 1-14, and 16-21) will minimize impacts to WBP and that

[badkitty] Autopsy results..

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

To: badkitty@groups.electrincembers.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 Duvuvuei, 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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"Science affects the way we think together."

Lewis Thomas

Clark's Nutcracker and Whitebark Pine: Can the Birds Help the Embattled High-Country Pine Survive?

*"I saw today a Bird
of the woodpecker kind
which fed on Pine burs its
bill and tale white
the wings black every other
part of a light brown, and
about the size of a robin."*

—William Clark, Lemhi Pass,
Aug. 22, 1805.

Whitebark pine (*Pinus albicaulis*) is found on the cold, steep, wind-lashed ridges of the high northern Rockies, Cascades, Olympics, and eastern Sierra Nevada. Its gnarled forms are a familiar sight to mountain climbers and high-country backpackers. Whitebark pine requires full sunlight to germinate and thus is an early colonizer of burns and other disturbed sites. At lower elevations, it is found intermixed with lodgepole pine and Douglas-fir. Near treeline, it occurs in small, scattered, nearly pure stands.

"Whitebark pine is a sentinel species in the high-mountain ecosystem," says Martin Raphael, research wildlife biologist at the Pacific Northwest (PNW) Research Station. Raphael recently collaborated on a study examining how the food-gathering efforts of Clark's nutcracker (*Nucifraga columbiana*), a crow-sized bird with a strong, sharp beak, help whitebark pine regenerate. "The tree plays a major role in mediating microclimates for other plants and animals, and its seeds are tremendously important in the diets of not only the nutcracker, but grizzly bears, ground squirrels, and jays," Raphael explains.



Teresa Lorenz

Researchers fitted Clark's nutcrackers with radio tags to study their role in distributing seeds from whitebark pine and caching the seeds in sites where they might germinate.

The tree has never been important commercially, and because it grows in the remote reaches of the West's high country, it has been sheltered from direct human influence. Yet whitebark pine is in trouble—it's experiencing declines of 45 percent across some of its range, says Raphael. "We're seeing tremendous mortality from the mountain pine beetle, which seems to be associated with climate change. The two go hand in hand: because warmer temperatures are putting stress on the trees, that makes them more susceptible to beetle attack."

IN SUMMARY

Whitebark pine inhabits some of the most pristine high-elevation areas of the West. Despite being protected from direct human influence, the tree is declining from indirect effects of fire suppression and climate change. As a keystone species, its decline has widespread ramifications. Successful restoration requires understanding the behavioral ecology of Clark's nutcracker, a bird that plays a key role dispersing whitebark pine seeds.

Until now, little quantitative information existed about the nutcracker's home ranges, seed transport habits, and caching behaviors. A team led by Teresa Lorenz, a master's student at Utah State University, and collaborators Martin Raphael and Carol Aubry of the USDA Forest Service, used radio telemetry to track the movements of 54 Clark's nutcrackers in the Olympic and Cascade Mountains over three seasons. They found that about half of the birds gathered seeds from outside their home ranges and that some flew up to 20 miles to forage, much farther than previously reported. Most seed was cached in microsites where it could not germinate. Nutcrackers also collected ponderosa pine seeds and were more effective in dispersing these to suitable sites than they were in dispersing whitebark pine seeds. This information can be used to focus restoration efforts, and may help managers refine seed-zone boundaries and identify the likeliest regeneration sites.

Fire suppression is the underlying dynamic that set the tree on its current course. Historically, whitebark pine thrived in the mixed-severity wildfire regime that once prevailed. Severe stand-replacing fires enabled the pine to colonize burned lands; light surface fires killed understory spruces and firs and gave the young pines a competitive advantage. With less frequent fires, spruce and fir gained a toehold, and they are now on their way toward supplanting whitebark pine across much of its lower elevation range. White pine blister rust and mountain pine beetle are attacking the stands that remain.

The pine's large, nourishing seeds feed many wildlife species, notably the Clark's nutcracker, which propagates the tree by caching its seeds in the ground. Other species that eat the seeds include woodpeckers, jays, ravens, chickadees, nuthatches, finches, chipmunks, tree and ground squirrels, and mice. The seeds also provide autumn food for grizzly bears and black bears, especially in the Rockies; whitebark pine communities near Yellowstone National Park and in northeastern Washington are designated as critical grizzly bear habitat.

The tree's cones are indehiscent—they don't open in the fall as do the cones of most other pines. In a fascinating co-evolved relationship, whitebark pines are propagated by the Clark's nutcracker. The nutcrackers flock around whitebark pine stands in autumn as the cones ripen and use their sharp, strong bills to hammer into the tightly closed cones and dig out the seeds. "You can see the cone chips flying,"

says wildlife biologist Teresa Lorenz, who has uncovered valuable new information on the bird's foraging and seed-caching habits. Advised by Raphael, Lorenz conducted her research while a master's student at Utah State University.

To cache their seeds in the ground, the birds swipe a shallow trench with their bills and deposit them. They also cache seeds above-ground next to rocks, among tree roots, near fallen logs or branches, and under slips of bark. The nutcrackers can cache thousands of seeds in a season and use their remarkable spatial memory to retrieve them. After a year or two, some of the ground-cached seeds that

aren't retrieved germinate, initiating the next generation of whitebark pine.

The bird's range is about three times as large as that of the trees, and its varied diet includes other conifer seeds (nutcrackers are particularly fond of ponderosa pine), insects, spiders, and even small mammals and amphibians. So the nutcracker apparently doesn't need the whitebark pine to survive, but the tree does seem to depend on the bird. Although other wildlife feed on whitebark pine seeds (squirrels can pose major competition to the nutcrackers), the caching of seeds by nutcrackers is the primary way—perhaps the only way in nature—that whitebark pine seeds encounter soil in which they can germinate.



KEY FINDINGS



- Clark's nutcrackers foraged widely for whitebark pine seeds but transported nearly all of them back to the home ranges for caching. Thus natural regeneration should be more abundant within nutcrackers' home ranges than outside them.
- Nutcrackers transported seeds over much longer distances than previously observed. The caching and germination of seeds from distant trees might produce even more genetic mixing in whitebark pine populations than previously known, resulting in greater homogeneity across the landscape.
- Nutcrackers also collected and cached ponderosa pine seeds. In fact, the birds were more effective dispersers of ponderosa pine than whitebark pine, placing more ponderosa pine seeds in habitats and microsites where they were likely to grow.
- Nutcrackers cached most seeds of both whitebark pine and ponderosa pine in unsuitable habitats for germination.



Teresa Lorenz

Whitebark pine is facing multiple threats across its range. In lower elevations, fire suppression has allowed spruce and fir to edge out whitebark pine. At higher elevations, white pine blister rust and mountain pine beetles are taking a toll on the pine

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HOW EFFECTIVE ARE THE BIRDS?

Given the pine's precarious status, the Clark's nutcracker is a high-priority study topic. Lorenz began her research in 2006, conducting the first quantitative study of Clark's nutcracker habitat use and cache-placement preferences.

The question that guided her research, Lorenz says, was, How effective are these birds in regenerating whitebark pine? "If we have stands that are dead or dying, should we plant seeds? Or plant seedlings? Or do nothing and

let the birds take care of it? Evolutionarily, the birds' job was to reseed whitebark pine. How much can we rely on birds to do this work of restoring?"

From April 2006 to September 2009, Lorenz and her team captured and radio tagged 54 nutcrackers at eight sites in the Olympic and Cascade Mountains, and tracked the spatial patterns of their foraging, caching, and nesting. They found that half of the birds remained year round near the capture site on fairly discrete home ranges, leaving these

ranges only in autumn to harvest seeds from distant pine stands. These the researchers classed as resident birds. The other half left the study area within a month or two of capture and were classed as emigrants.

Nutcrackers do all their seed foraging and caching during late summer through autumn, as cones ripen. During this time, Lorenz's team spent up to 7 hours a day, 4 days a week, watching individual birds, learning where they collected their seeds and where they cached them.

STRONG HOME TIES

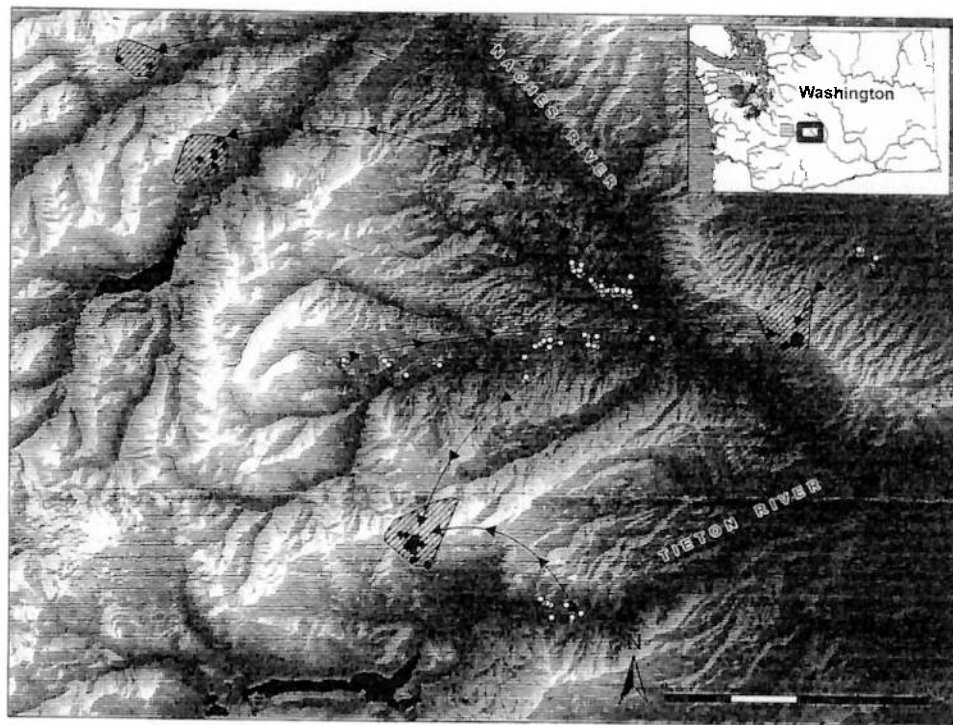
The team was the first to demonstrate that resident nutcrackers are strongly tied to a single home range. Previous studies had suggested that the birds followed the ripening cone crop uphill in the summer and fall, caching their seeds near the parent trees, and then moved back downhill to a winter range and lived there until spring.

"We didn't find that at all," says Lorenz. "I remember on Labor Day 2006, one of my birds collected seeds and went back to its home range to cache them. I thought, My gosh, he's taking the seeds back! They're not migrating; they're going back to their home ranges with the seeds! I watched that bird closely for a week to be positive he was really doing that."

The team watched the birds fetch seed multiple times a day from as far away as 20 miles—much farther than the previously reported 8 miles. The birds worked tirelessly, flying up to 5 hours a day and sometimes topping several ridges on each trip. "It's as if they're going to the grocery store," Lorenz explains. "They're going out and buying their groceries and bringing them home. They're not living where the groceries are."

The birds in this study cached their seeds in protected places at the driest, lowest elevation sites within their range. In contrast to previous observations, the birds placed their seeds more often in aboveground than in belowground sites. They avoided caching seeds on exposed places such as burns.

A bird's choice of a cache site, explains Lorenz, may represent a tradeoff between the risk of losing the cache to squirrels or mice (which argues for placing seeds out in the open) and the risk of being killed by a predator (which argues for placing them in protected sites). "These nutcrackers selected sites that compromised the safety of their food stores but secured their personal safety," Lorenz says.



This map shows flights by Clark's nutcrackers as they transported ponderosa pine seeds from harvest sites (white circles) to cache sites (black circles). The arrows indicate direction of seed transport to the birds' home range (striped polygons). Seed harvest stands occurred between 2,100 feet and 2,600 feet in elevation while home ranges were located between 4,000 feet and 6,100 feet in elevation.

Some birds clearly do cache seeds on bare or exposed sites, says Raphael, but it's notable that Lorenz didn't see it in her study. "While this would be statistically rare, even a rare event can have ecological consequences. The birds cache so many seeds that some do end up on exposed ground, and some of these establish and grow."

The value of Lorenz's finding, he says, is that it demonstrates the low likelihood that seeds will end up in a good germination spot. All told, birds placed only about 15 percent of whitebark pine seeds in places where germination was possible. The rest they either buried in lower elevation habitats (notably

ponderosa pine stands) or cached above ground in the whitebark pine canopy.

Their propensity to cache seeds in relatively snowfree places (making food accessible year round) meant that the birds were more effective seed dispersers for ponderosa pine than for whitebark pine. They cached more than half their ponderosa pine seeds in the ponderosa pine zone, and more of the seeds were cached in the ground at these lower elevations.

This is not good news for the whitebark pine. Of whitebark pine seeds cached in soil, none apparently germinated. As whitebark pine declines in the Northwest, ponderosa pine may



Teresa Lorenz

Researchers observed that Clark's nutcrackers tended to cache seeds aboveground rather than belowground.



Teresa Lorenz

The seeds that the nutcrackers did cache belowground tended to be at lower elevation sites, frequently in stands of ponderosa pine.

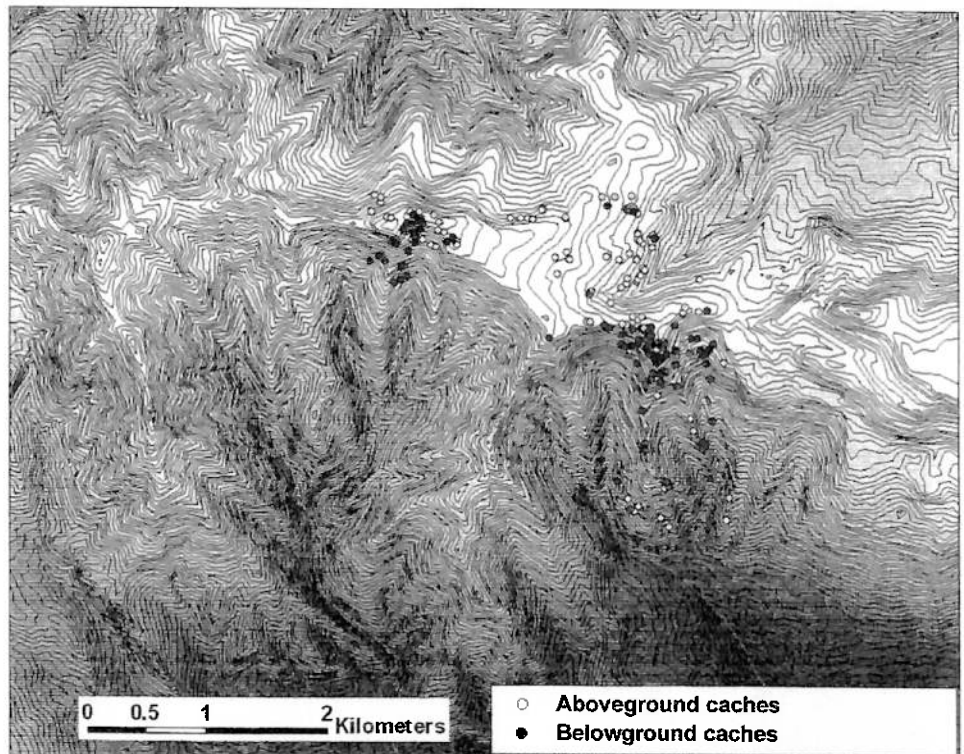
become more important food for nutcrackers, which might make them more likely to select home ranges in ponderosa pine stands, resulting in even fewer whitebark pine seeds maturing into trees.

Moreover, birds don't always go out of their way to gather whitebark pine seeds. "Some of my birds didn't harvest whitebark pine even if it was there," says Lorenz. "They focused on ponderosa pine probably because it was closer to their home range." Because both trees are "masting" species, producing a big cone crop every few years and lean crops in between (in fact, whitebark pine in Lorenz's study area didn't make a cone crop at all in 2008), a broad diet is a survival advantage for the birds, but it makes them less efficient in regenerating whitebark pine because they don't focus exclusively on it.

The nutcracker isn't the only one eating whitebark pine seeds. Squirrels cut the cones from pine trees and hoard them in piles called middens. Squirrel middens are unlikely places for seeds to germinate and grow. But chipmunks and deer mice may pilfer seeds from both squirrel middens and nutcracker caches and re-cache them in the ground near shrubs, where they may germinate. This secondary dispersal, say the researchers, may be more important than previously thought.

Lorenz, now working on her doctorate, plans to test this hypothesis by burying whitebark pine seeds (she'll pry open the cones with a sharp knife) and seeing whether chipmunks dig them up and re-cache them. "I'm going

to act like a nutcracker for the next 2 years," she says with a smile. "I have 1,500 cones in my living room right now that I stole from the squirrels, and it's taking me forever to extract the seeds."



This map shows above- and belowground seed caches of three Clark's nutcrackers over 3 years at the Cash Prairie site in the Cascade Range, Washington.

HELPING THE BIRDS

The nutcracker's caching behavior makes it clear that nutcrackers alone probably can't bring whitebark pine back from the brink. The system is being stressed by bark beetles, blister rust, and a warming climate, says Raphael. "Nutcrackers probably can't overcome these trends. The birds' caching of seeds is absolutely necessary, but it's not sufficient to recover the pine."

The nutcrackers' fidelity to their home ranges suggests that natural regeneration will be most abundant in areas where nutcrackers live. Knowing this, managers might target their restoration efforts in other areas where stands are smaller and more isolated.

The study confirms previous findings that seed zones for whitebark pine are relatively large. Because of natural selection, trees growing within a given area—a seed zone—will produce offspring that grow best within that area. Generally, the farther seeds are naturally dispersed, the larger the seed zone. Larger seed zones make it easier and cheaper to collect seed for regeneration.

The nutcrackers' surprisingly long foraging distances suggest that whitebark pine has spread its genes widely, resulting in a relatively homogeneous landscape-wide population (although it may show diverse local genetic patterns). The birds' long-distance seed dispersal may also help whitebark pine adapt more quickly to a warming climate.

The study was also the first documented evidence of the role of Clark's nutcrackers in disseminating seeds of ponderosa pine, which are also dispersed by wind and rodents—suggesting that ponderosa pine may be regenerating in yet-unknown spatial patterns. Moreover, say the researchers, because ponderosa pine seeds are important food for nutcrackers in Washington and Oregon, "the success of whitebark pine restoration may be irrevocably linked to the conservation of low-elevation ponderosa pine," says Lorenz.

Lorenz's study, says Raphael, provides important new information on an ecosystem that needs urgent attention. "Before Teresa did this work," he says, "we had no radio-telemetry information that told us how far these birds move. What she found alters our thinking on the genetics of this tree—it mixes up locations to a much greater degree than we appreciated before. That's a big thing, and it has important implications for restoration efforts."



LAND MANAGEMENT IMPLICATIONS



- Most seeds cached by nutcrackers will not germinate. Relying on nutcracker dispersal alone for restoring the whitebark pine ecosystem is not likely to be effective.
- Nutcrackers cached most of their seeds within their home ranges, suggesting restoration of whitebark pine outside nutcracker home ranges may be an appropriate priority.
- Seed zones for whitebark pine may be even larger than previously assumed. This could simplify and lower the cost of collecting seeds for artificial regeneration.
- Conserving lower elevation ponderosa pines—an important food source for Clark's nutcrackers—may be essential to restoring whitebark pines, which depend on the nutcrackers for regeneration.



Teresa Lorenz

Researchers learned ponderosa pine seeds are an important food source for the nutcracker. Conserving lower elevation ponderosa pine stands may be instrumental to conserving higher elevation whitebark pines, which depend on the nutcracker for seed dispersal.

"Alpine or backcountry skiing among the whitebark pine stands conveys a special thrill; you are indeed in the highest place, otherwise inaccessible, where survival in winter is a challenge to every plant and animal."

—Diana Tomback, Stephen Arno, and Robert Keane, in *Whitebark Pine Communities: Ecology and Restoration*

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WRITER'S PROFILE

Gail Wells is a science writer based in Corvallis, Oregon. She is the author of *The Tillamook: A Created Forest Comes of Age* (2nd ed. 2004) and coauthor of *Lewis and Clark Meet Oregon's Forests: Lessons From Dynamic Nature* (2001).



Science

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"Science affects the way we think together."

Lewis Thomas

Woodpecker Woes: The Right Tree Can Be Hard to Find



Teresa Lorenz

A female black-backed woodpecker perches at a nest excavated in a live ponderosa pine in central Washington. Although the tree diameters used by this species for nesting differed (ranging from 8 to 34 inches), it consistently selected nest sites with softer interior wood.

"In order to see birds, it is necessary to become part of the silence."

—John Keats

Somewhere in Washington's eastern Cascade Range a bird perches motionless against a burned tree. It's an American three-toed woodpecker (*Picoides dorsalis*), sporting black back feathers, a white mustache stripe, and a yellow cap. About the size of a large banana, the bird has evenly spaced white flecks on the sides of its chest and on its primary and secondary feathers.

The bird was extracting beetle larvae from another burned tree when a larger, louder black-backed woodpecker (*P. articus*) drove it away. But here, on this burned tree, it drums, "This one is mine. Stay away."

Soon it will pick a spot on the tree, say 30 feet above the forest floor, and bore rapidly into the wood with its chisel-like bill until it excavates a deep pocket. The bird and its mate will roost and nest in this safe place until its favorite food runs out, perhaps in 4 or 5 years. By then, another forest fire might provide a new supply of wood-boring insects.

IN SUMMARY

Woodpeckers and other cavity-excavating birds worldwide are keystone species. These birds excavate their nests out of solid wood, and because their nests are often well protected against predators and the environment, other species use and compete for their old, vacant nests. The presence of cavity-excavating birds in forests has far-reaching effects on species richness and ecosystem health.

Given the species' importance, Teresa Lorenz, a research wildlife biologist with the U.S. Forest Service Pacific Northwest Research Station wanted to find out why cavity-excavating birds do not use many trees seemingly suitable for nesting. This puzzle has eluded researchers for decades. Lorenz and her colleagues also wanted to know what role wood hardness plays in the birds' nest site selection.

The resulting study in the eastern Cascades of Washington found that cavity-excavating birds preferred to nest in trees with significantly softer interior wood. The researchers also found that at-risk species were nesting within burned areas where up to 96 percent of the trees had unsuitably hard wood. This suggests that many trees and snags previously considered suitable for cavity-excavating birds actually may not be.

In dry forests, prescribed mixed-severity fire may be a useful tool for creating suitable nesting habitat for cavity excavators.

In the woodpeckers' absence, other birds or small mammals like owls, squirrels, and bats move in. The new tenants disperse seeds and spores that help new plants and fungi grow. When the dead, burned trees—also called snags—fall to the ground, wood-living bees and wasps take up residence. Fungi and lichens flourish on the fallen tree's gnarly surface, and occasionally a marten hides behind the log.

Because of the woodpeckers' crucial role in maintaining healthy forests, researchers want to understand how these cavity-excavating birds choose trees to nest in. When forest managers know what these birds like, they can take steps to ensure that forests have these kinds of trees.

"Woodpeckers are ecosystem engineers," says Teresa Lorenz, a research wildlife biologist with the Pacific Northwest Research Station. "Many small animals compete for their vacated nests because they are so protected from the elements and other predators."

Ecosystem engineers are organisms that significantly modify, maintain, or destroy a habitat. In the woodpeckers' case, the species help build and maintain a habitat for other species by excavating nests in live and dead trees. When forest managers find many different woodpecker species in a forest, it often signals the presence of a thriving and diverse community of plants and animals.

KEY FINDINGS

- Across 818 snags in Yakima, Kittitas, and Chelan Counties in Washington's eastern Cascade Range, trees not used by birds had wood five times harder than trees that were. Such trees could not be used by birds simply because their wood was too hard for the birds to excavate.
- Within burns used by at-risk woodpeckers, the majority (86 to 96 percent) of seemingly suitable trees contained unsuitably hard wood; wood hardness limits nest site availability for these declining species.
- Researchers found no reliable visual cues to distinguish between suitable and unsuitable trees. Currently, the most effective management solution is to provide large numbers of snags, which can be difficult without the aid of fire.
- In dry forests, a mixed-severity fire that kills trees is an important but underappreciated strategy for providing enough snags for cavity-dependent species. Low-severity prescribed fires may not provide enough snags for these species.
- Suitable snags are limited, such that snag availability drives landscape-level habitat-selection by some species. For example, white-headed woodpeckers selected severely burned patches for nesting, which was initially puzzling because this species does not characteristically forage in burns.

Cavity-nesting birds typically nest in recent burns. More than 50 years ago, studies suggested that woodpeckers picked trees solely based on external tree- or habitat-level factors, like the size of the tree, the tree species, or what the vegetation cover is like near the nest.

Other studies pointed to wood decay, but used only visual indicators to assign a snag decay class as a proxy for measuring this. Lorenz felt there was a missing piece: few studies actually measured wood inside the trees where cavity-excavating birds had chosen to nest.

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A pine marten looks out of a pileated woodpecker nest cavity. Many species require or prefer vacated woodpecker cavities, but cannot excavate the cavity themselves. Thus, they rely on woodpeckers to construct habitat for them.

Teresa Lorenz

Matsuoka's Method

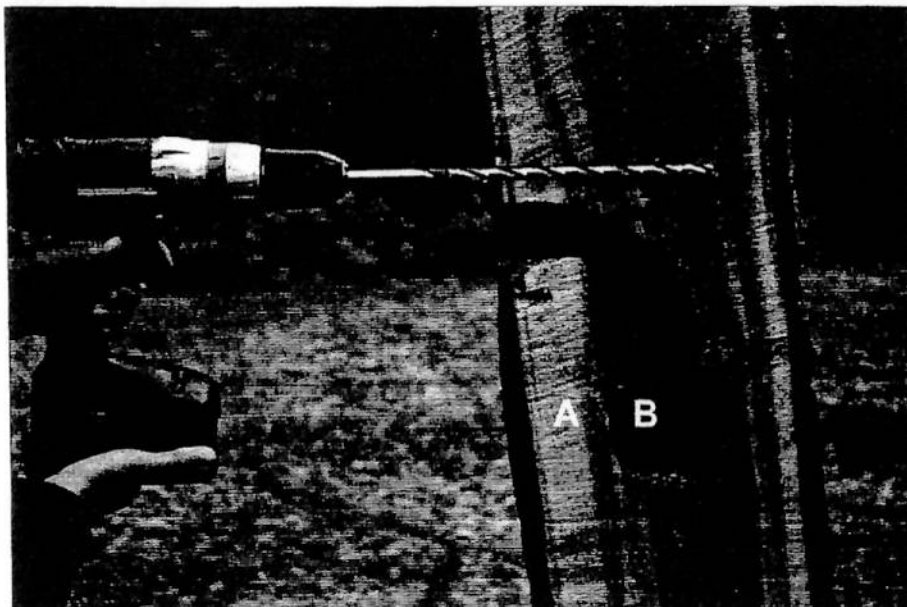
The idea for the study came to Lorenz and her colleagues in summer 2011, when they were investigating how far woodpecker nestlings wandered from their nests soon after they fledge. Using hole saws, they drilled into trees to get to the nestlings, to band them. "We noticed an enormous variation in the thickness of the wooden plug," Lorenz says. "Sometimes the nestling would be just inside the bark of the tree. Other times we had to drill through 4 inches of wood. We had all these hypotheses as to what was going on."

A colleague suggested that the variation could be due to the properties of the wood in the tree. Intrigued, they checked the literature. What if wood hardness had something to do with the birds' preference when looking for trees to nest in? Lorenz and her colleagues did not find many studies that addressed this question. "We were surprised that nobody had considered that this wood inside the tree was influencing where the birds were nesting," Lorenz says. So, she decided to investigate the question for her Ph.D. dissertation at the University of Idaho.

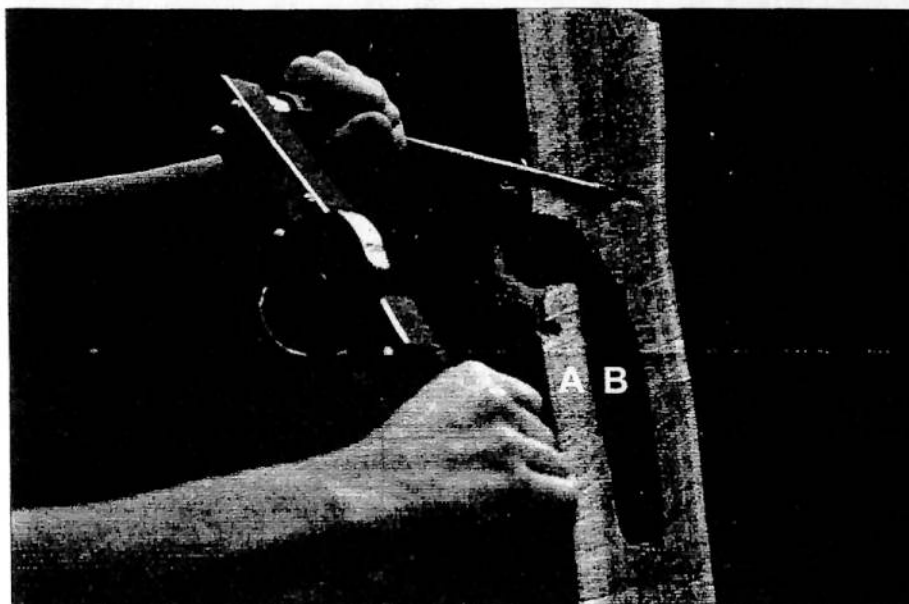
The problem was there weren't many reliable methods for measuring wood hardness in a forest setting. "But we found an obscure article in the *Japanese Journal of Ornithology* and this guy had figured out an ingenious way to measure the hardness of wood inside a tree, using a cordless drill, a foot-long drill bit, and an increment borer, without destroying the nest or harming the tree," Lorenz says.

An increment borer is a tool used by foresters and other researchers to extract a section of wood tissue so they can count a tree's annual rings and determine its age. Japanese researcher Shigeru Matsuoka's method involves inserting this tool into a pre-drilled hole above the nest cavity opening. The torque required to spin the increment borer would represent wood hardness. With the most important aspect of her field methods squared away, Lorenz set out with colleague Philip Fischer to gather field data in the eastern Cascade Range in Washington.

Lorenz had selected six species of cavity-excavating birds for the study. She picked three strong excavators: the three-toed woodpecker, the black-backed woodpecker, and the hairy woodpecker. She also picked a weaker guild of excavators, namely the northern flicker (*Colaptes auratus*), the white-headed woodpecker (*Picoides albolarvatus*), and Williamson's sapsucker (*Sphyrapicus thyroideus*).



Teresa Lorenz



Teresa Lorenz

This photo shows the longitudinal section of an American three-toed woodpecker (*Picoides dorsalis*) nest and the procedure the study used to quantify wood hardness. First, the researchers use a drill to create a small hole about one-third inch in diameter above the nest cavity opening (top). Then they record the torque required to spin an increment borer into the predrilled hole (bottom). The area marked "A" represents the nest sill, and the area marked "B" represents the nest cavity body.

They searched for nests in all major forest types for 3 years from March to July, 2011 through 2013, hiking through ponderosa pine, Douglas-fir, and western hemlock in lower elevations and through higher elevation forests of grand fir, subalpine fir, and western larch. Lorenz and Fischer located adult birds by broadcasting playbacks of their calls and drumming. "Then, we followed the adults until they led us to their nest cavities," Lorenz says. They marked the

locations of occupied nests on portable GPS units. If they noted fresh woodchips on the ground surrounding the nests, they marked those as current-year excavations. They found nests in forest patches ranging from unburned to severely-burned.

Lorenz and Fischer covered a lot of ground. Each of their 10 study sites were 1,483 to 7,413 acres in size. "You get in really good shape," Lorenz says.

Soft Pockets

Each carrying about 30 pounds of equipment, Lorenz and Fischer returned in summer to make their measurements. After ensuring the nests had been vacated by the birds, the researchers would scale a tree on climbing ladders to measure wood hardness. They drilled 2 inches above the nests because Matsuoka's study suggested this spot would be representative of the excavated wood.

"In the beginning, we had assumed that wood at the nests would be entirely soft, but that wasn't the case," Lorenz says. "There was some variability when we first started drilling into the trees. Some had hard surfaces. But when you get into the tree a bit, that's when you find these soft pockets. Other times, the soft pockets were close to the surface of the tree, and other times the tree was soft from the get go."

To determine if a tree's external features are reliable indicators of interior wood hardness, the researchers measured wood hardness in random trees within different decay classes.

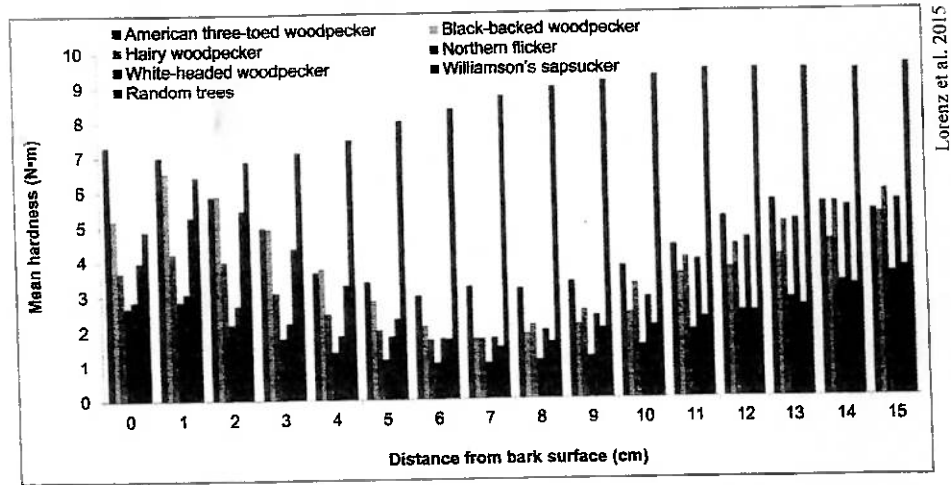
Then the researchers measured vegetation features that were hypothesized to influence cavity-excavating birds' nest site selection in past studies, such as diameter at breast height of the nest tree; nest and tree height; orientation of the nest cavity entrance; proportion of the ground covered by shrubs; tree and snag density at the nest sites; and tree species.

For nests found in snags, they examined the remaining bark, tree growth form, and other features to determine the tree's species.

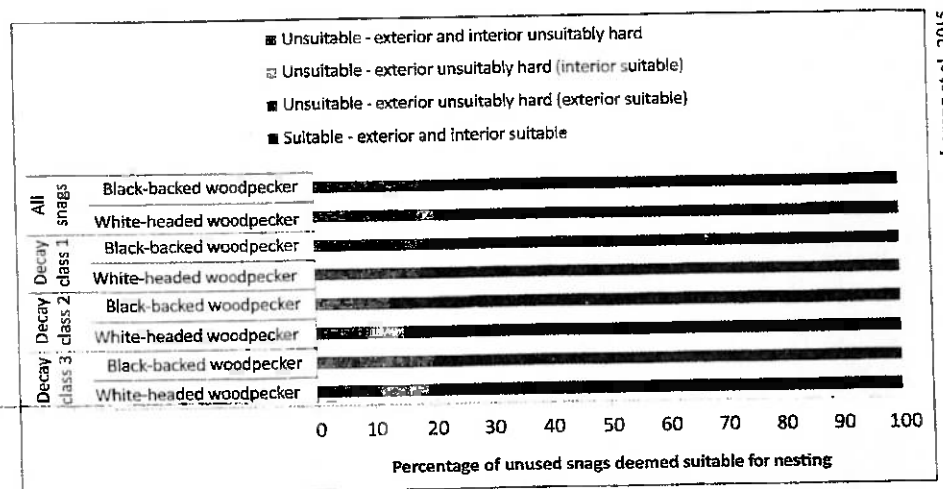
"It was a pretty brutal field season," Lorenz says. "We worked from 6 a.m. to 4 p.m. And it got really hot in these sites."

Lorenz and Fischer also used remote sensing data. To estimate prefire canopy cover at nest sites found in snags, they used gradient nearest neighbor classified Landsat satellite imagery captured between 2 and 8 years prior to each fire.

Lorenz was concerned about seeing an effect in nature, measuring it, but finding a lot of variability. "What if we went to another tree and that pattern didn't hold?" Lorenz says. "But in this study, we were able to measure so many trees that we were confident that the effect we were seeing was real. And it has major management implications."



Mean hardness at nests for six species of woodpecker compared to random sites in central Washington, from 2011 to 2013.



A small percentage of snags are suitable for woodpecker nesting. This chart shows the percentage of 360 unused snags in black-backed woodpecker and white-headed woodpecker nesting territories that were deemed suitable for nesting, based on wood hardness, in central Washington, from 2011 to 2013.

Drawn to Snags

Lorenz and her colleagues found that cavity-excavating birds preferred to nest in trees with significantly softer interior wood. They found that across 818 snags, trees not used by birds had wood five times harder than trees that were. These trees could not be used by birds simply because of the birds' physical limitations in pecking ability.

They found that at-risk species, namely the black-backed and the white-headed woodpeckers, were nesting within burns that contained 86 to 96 percent of trees with unsuitably hard wood. This suggests that past studies that did not measure wood hardness counted many sites as available to cavity-excavating birds when actually they were unsuitable. "By not accounting for wood hardness, managers may be overestimating the amount of suitable habitat for cavity-excavating bird species, some of which are at risk," Lorenz says.

In their study plots, the researchers did not find reliable visual cues to distinguish between suitable and unsuitable trees. Snag decay class was a poor indicator of internal wood properties—and this was not the first study to demonstrate that fact, although it was the first study to do so in ornithology (past studies had been done by foresters and published in forestry journals).

"Currently, the best solution we can recommend is to provide large numbers of snags for the birds, which can be difficult without fire," Lorenz says. According to the researchers' calculations, if one of every 20 snags (approximately 4 percent) has suitable wood, and there are five to seven species of woodpeckers nesting in a given patch, approximately 100 snags may be needed each year for nesting sites alone. This does not account for other nuances, like the fact that most species are

territorial and will not tolerate close neighbors while nesting, or the fact that species like the black-backed woodpecker need more foraging options. Overall, more snags are needed than other studies have previously recommended.

Based on their results, Lorenz and her colleagues see the critical role that mixed-severity fires play in providing enough snags for cavity-dependent species. Low-severity prescribed fires often do not kill trees and create snags for the birds. In addition to benefiting the cavity nesters, a mixed-severity prescribed burn could also aid species that, historically, did not prefer to nest in snags. During their field work, Lorenz and Fischer observed that white-headed woodpeckers, a species traditionally associated with old-growth forest, used prescribed burns presumably because of shortages in suitable nest sites.

"I think humans find low-severity fires a more palatable idea. Unfortunately or fortunately, these birds are all attracted to high-severity burns," Lorenz says. "The devastating fires that we sometimes have in the West almost always attract these species of birds in relatively large numbers."

Many studies have shown that a severely burned forest is a natural part of western forest ecosystems. Snags from these fires attract insects that love to burrow beneath charcoal bark. And where there are insects, there are birds that love eating these insects.

Lorenz and her colleagues stress that providing snags that woodpeckers can excavate is crucial for forest ecosystem health in the Pacific Northwest, where more than 50 wildlife species use woodpecker-excavated cavities for nesting or roosting.

"This study was just the beginning of what I hope will be decades of research," Lorenz says. Picking up on what she learned in this study, Lorenz is now collaborating with Forest Service colleague Michelle Jusino to investigate a kind of fungi that follows forest fires. "There is some mechanism by which the death of a tree somehow enables some species of fungi to decay the wood," she says. The research is bound to take her back into the forests of the Pacific Northwest, where woodpeckers follow forest fires in a timeless cycle of change.

*"The powerful play goes on
and you may contribute a verse."*

—Walt Whitman, *Leaves of Grass*

LAND MANAGEMENT IMPLICATIONS

- Providing snags that woodpeckers can excavate is important for forest ecosystem health in the Pacific Northwest, where more than 50 wildlife species use woodpecker-excavated cavities for nesting or roosting.
- Mixed-severity prescribed-fire may be useful in creating breeding habitat for the white-headed woodpecker, a species traditionally associated with old-growth forest.



Teresa Lorenz

The prescribed burn conducted in this stand flared up in patches, creating a mosaic of burned and unburned trees (a mixed severity burn) that is still used by white-headed woodpeckers and black-backed woodpeckers 10 years after the fire. Tree death is usually required to initiate the process of wood decay—which softens the wood, making it suitable for woodpecker excavation.

For Further Reading

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Writer's Profile

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