

UNIVERSITY OF SCOTLAND, notes: "Although I have never actually witnessed this behaviour, I have some evidence that it does occur and have seen plunge marks along wooded-field edges. Usually small bits of feathers betrayed the species of owl and in one instance, drops of blood indicated a successful capture. I would suggest that in severe winters when snows are deep and alternative foods are scarce, subnivean capture of small mammals are more frequent than in mild years. An eyewitness account of snow plunging conveyed to me by a local man confirmed the existence of the behaviour. In this instance, an unsexed Barred Owl was observed hunting along a wooded-field edge during daylight hours in 1985. Of three plunges made by this owl, only one was successful in the capture of an unidentified small mammal" (pers. corres., 6 September 1987).

Upon enquiry, Dave Johnson, who studies Barred Owls in north-central Minnesota, responded as follows: "Have never actually witnessed a Barred plunge, but have one observation from Jan. 1983, Becker County, MN, of a nice plunge hole made by a Barred. It was near one of my nest boxes, and I had seen a Barred in the vicinity on four occasions during that week. I have looked for Barred plunge holes for five years now. The plunge hole occurred in a small marsh pocket (30 yards across) in a northern hardwood forest type, where overhanging trees provided a perch. I recall snow depths of 15-18 inches in the marsh pocket" (pers. corres., 3 September 1987). The late Don Follen, a Wisconsin owl student, had this to say: "Snow plunging: I've seen Bd's [Barred's] on several occasions in the snow up to their pits. This is of course soft fluffy snow" (pers. corres., 24 August 1987).

Despite our many years in the field in winter in southeastern Manitoba looking for owls, Herb Copland and I have only three indications of snow-plunging by Barred Owls. Late in the afternoon of 4 January 1981, along the Glen road east of East Brantree, we found fresh signs of snow-plunging by a bird of Barred Owl size. There were at least six plunge-holes in the snow over a grassy field. Except for the small size, they resembled marks made by Great Gray Owls. The holes were close to trees. Again, and in the same vicinity, on 11 January 1981 we saw similar plunge-holes in the afternoon, and then at 8:00 p.m. a Barred Owl came out and perched in a nearby tree. We assumed that it was the bird that had made several Barred Owl-size plunge-holes at a new site several kilometres away. At one plunge-hole there was an imprint of the owl's face showing the bill, just as we have seen at numerous Great Gray Owl plunge-holes. This imprint was the size of a Barred Owl's face.

In our experience, Barred Owls are seldom seen here, especially in winter. The species, as noted by Johnsgard, "is essentially a semi-nocturnal to nocturnal hunter."³ Apparently less bold and seemingly more restricted to hunting within woods than Great Gray Owls, only six Barred Owls have been seen by Herb Copland and myself over the past 20 winters. Jim and Patsy Duncan, on the other hand, recorded three sightings of Barred Owls in winter 1986-87: one at 5:00 p.m. - 12 December; one at 2:22 p.m. - 2 February; and one at 4:49 p.m. - 16 March. The latter bird, which they captured when it came into a lure, was reported as noticeably thin (pers. corres., 1987). Herb and I captured one at 3:15 p.m. on 4 February 1979, northeast of Lac du Bonnet. Upon seeing what we assumed

to be a Great Gray Owl back some distance from the road in a grove of aspens, we set out to capture the bird, on the third cast of the lure, the owl came out from the trees in pursuit of it. We were surprised to see, when it was close, that it was a Barred Owl. It turned away at the last minute, but landed nearby and a moment later came in to a live mouse and was netted by Herb. Its belly plumage was wet and there was even a little ice on some parts. We guessed that it had roosted in wet snow in a tree cavity. It was kept in the car long enough to dry out its plumage before we released it.

I am particularly grateful to Richard W. Knapton for allowing me to use his observations of the Boreal Owl. Thanks for their information are also owing James R. Duncan, Patricia A. Duncan, Mark F. Elderdin, David H. Johnson and the late Donald G. Follen, Jr. For congenial companionship on owl forays, I am indebted to Herbert W. R. Copland.

"Recently, estimates on the number of species [of plants and animals] on earth have been revised dramatically upward, from around 5 or 10 million to between 30 and 50 million. The point is, no one knows. Only 1.4 million species have been classified." *Verlyn Klinkenberg, Audubon Jan-Feb 92*

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FOREST MANAGEMENT AND CONSERVATION OF BOREAL OWLS IN NORTH AMERICA

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ABSTRACT.—Boreal Owls (*Aegolius funereus*) in North America occur throughout the boreal forests of Canada and Alaska and in subalpine forests of the Rocky Mountains north of central New Mexico. A recent assessment of Boreal Owl conservation status in the western mountains of North America suggested that Boreal Owls were not in immediate peril. However, in the long-term and in selected local areas, Boreal Owls likely face conservation problems. This conclusion reflects the hypothesized response of Boreal Owls to the type and pattern of forest harvest that occurred in the past and may occur in the future. Over the last 40 yr, a majority of timber harvest occurred as clear-cutting that removed the older, more diverse forest stands. Forest structure influences the availability of suitable cavities, the quality of roost sites, the foraging movements of individual owls and prey availability. Components of mature and older forests are especially important to Boreal Owl habitat quality; the owls nest in large tree cavities and prey populations are most abundant in older forest stands. Clear-cut sites will remain unsuitable for roosting or foraging for a century or more and new nest trees will not develop in some situations for two centuries or longer. Timber harvest which maintains components of mature forest well dispersed across the landscape may be compatible with conservation of Boreal Owls. In particular, forest management must consider the consequences of management decisions across broad spatial scales and over a long-term horizon. Metapopulation modeling and experimentation through adaptive management will be necessary to develop timber harvest practices compatible with conservation of Boreal Owls.

KEY WORDS: forest management; Boreal Owl; *Aegolius funereus*; woodpeckers; small mammals; adaptive management.

Administración Forestales y Conservación de Búhos Boreal en Norte América

RESUMEN.—El Búho Boreal *Aegolius funereus* en norte américa ocurre en todas partes de bosques boreal en Canadá y Alaska y en bosques sub-alpino en las montañas Rocosas norte de centro Nuevo México. Una evaluación reciente del estado de conservación del Búho Boreal en las montañas del oeste en norte américa sugiera que el Búho Boreal no está en peligro inmediato. Sin embargo, en la larga duración, y en áreas seleccionadas en el local, Búho Boreal pueden encontrarse con problemas de conservación. Esta conclusión refleja la respuesta hipotetizada del búho boreal para el tipo y ejemplo de cosechas de bosque que ocurrió en el pasado y puede ocurrir en el futuro. En los últimos 40 años una mayoría de cosechas de madera ocurrió en el corte-completo que quito áreas de bosque maduros y de mas diversidad. La estructura de bosque influencia la disponibilidad de parcelas suficiente, la calidad de perchas, los movimientos de forraje de búhos solitarios, y la disponibilidad de cazar. Componente de bosques maduros y viejos son especialmente importante al hábitat del Búho Boreal: Los búhos hacen nidos en cavidades grandes de los árboles y poblaciones de cazar son mas abundante en parcelas de bosque viejas. Sitios cortados-completo se quedaran inconveniente para perchas o forraje para un siglo o más y árboles con nidos nuevos no se desarrollan en unos situaciones por dos siglos o mas. Cosecha de maderas que mantienen componente de bosques maduros bien dispersos a través el paisaje puede estar compatible con la conservación de Búhos Boreal. En particular la administración de bosques necesita considerar las consecuencias de las decisiones que hace a través de la escala de espacio amplio y sobre suficiente tiempo con perspectiva. Modelos de meta-población y experimentación a través de administración adoptivo va ser necesario para desarrollar costumbres compatible de cosechas de madera con conservación de Búhos Boreal.

[Traducción de Raúl De La Garza, Jr.]

The North American distribution for Boreal Owls (*Aegolius funereus*) forms a relatively continuous band extending from the Pacific to Atlantic

coasts in the boreal forests of Alaska and Canada (Godfrey 1986). South of the continuous transcontinental band, disjunct populations occur in the

Rocky Mountains extending into northern New Mexico (Palward et al. 1987, Whelton and Winski 1990). Throughout the owl occurs in a variety of forests: conifer and mixed-conifer (Bondrup-Nielsen 1978), temperate (Lane 1988) and subalpine (Hayward et al. 1993). The owl is intimately linked to the dynamics of these forests. In 1993, Hayward and V. distribution and abundance are strongly influenced by

How do population dynamics change? In this paper I provide a review of the impacts of forest management on Boreal Owls. I represent likely to influence the abundance of Boreal Owls, at the Rocky Mountains, may represent the most universally tied understanding of the population dynamics of Boreal Owls to various changes in forest dynamics is a critical step.

In the U.S., management of Boreal Owls come an important national Forest Regions. National Forest which represent south of Canada have as a "sensitive species." System, sensitive species whose population viability is a concern by a Regional Forest. I require special management to develop management for Boreal Owls (J. Friedlander 1994).

Unfortunately, the development of a sound management plan (Hayward 1994a). To develop a management plan for Boreal Owls, the ecological basis of the population (Bondrup-Nielsen 1978, al. 1992, Hayward et al. 1993) represents ecological questions, to directly address forest management or the

need thermal cover.

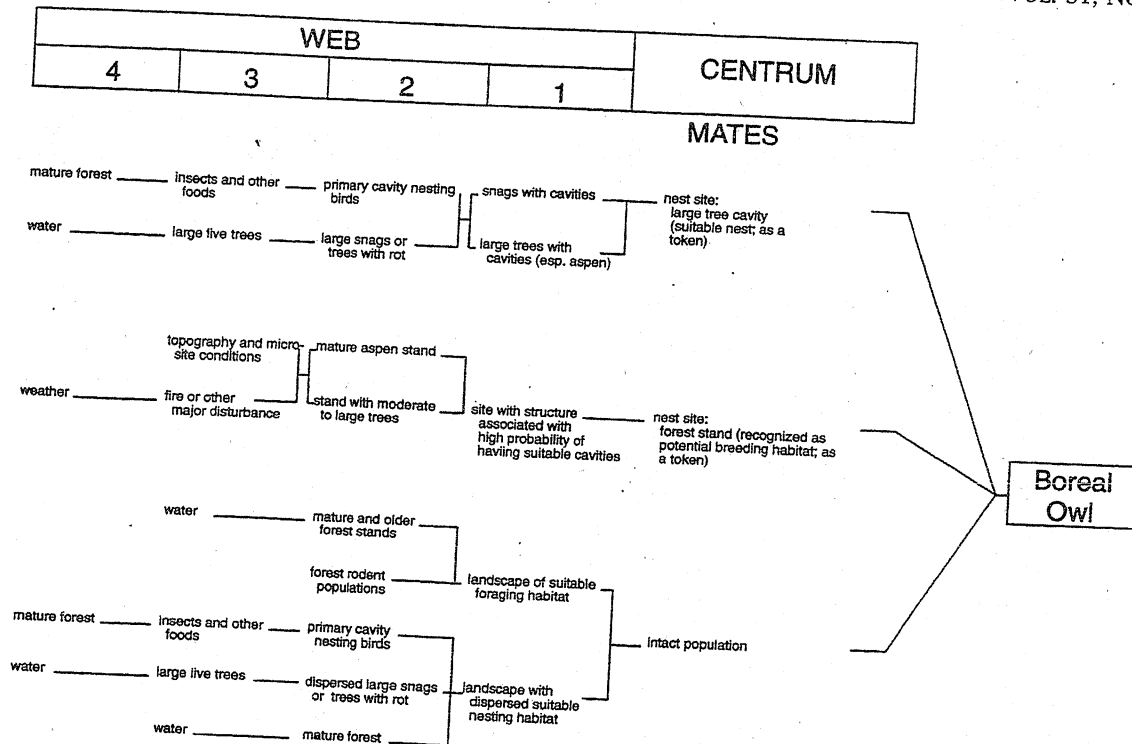


Figure 1. Envirogram (Andrewartha and Birch 1984) illustrating the relationship between Boreal Owls and specific components of the forest system. This portion of a larger envirogram (Hayward 1994b) focuses on Boreal Owl nesting ecology.

based more on efficiency in finding a cavity than increased survival after locating a nest.

The same studies in Idaho suggest that patch size may not be an important characteristic of nest stands. Nest stands ranged in size from 0.8 to 14.6 ha and averaged 7.6 ha.

Roosting habitat. Patterns of roosting habitat use also suggest these owls choose forests with particular structural features during certain times of the year. In Idaho, forest structure at summer roost sites differed substantially from paired random sites. Roost sites had higher canopy cover, basal area, and maybe most important, were significantly cooler microsites (Hotelling's T^2 , $P < 0.001$) (Hayward et al. 1993). In summer, and particularly in the southern portion of their range, Boreal Owls find roost sites to minimize heat stress. We witnessed owls gular fluttering and other behaviors associated with heat stress when the temperature was as mild as 18°C. I hypothesize that the elevational distribution of Boreal Owls in the Rockies may be determined, in part, by summer tempera-

tures and the availability of cool microsites for roosting. Forest structure, then, may influence the distribution of Boreal Owls through an interaction with limitation by heat stress.

Foraging habitat. A variety of evidence suggests that Boreal Owls in the Rockies forage principally in mature and older forest, especially spruce-fir forests (Hayward 1987). These observations are corroborated by evidence that red-backed voles (*Clethrionomys gapperi*) represent a dominant prey for Boreal Owls throughout their range in North America (Bondrup-Nielsen 1978, Palmer 1986, Hayward and Carlton 1988, Hayward et al. 1993). Red-backed voles are principally forest voles (Hayward and Hayward 1995). Our studies of small mammals in Idaho found redbacks were up to nine times more abundant in mature spruce-fir forest than other forest habitats (Hayward et al. 1993). The argument for the importance of mature forest for foraging stems also from observations of snow characteristics in openings, young forest and mature forests. Snow crusting is significantly reduced

in mature forests facilitating movement during critical winter months (Sonerud et al. 1986). Significant movement during warm winter months became severe.

An envirogram further illustrates the relationship between Boreal Owl fitness and abundance and features of the forest system. The envirogram illustrates the relationship between Boreal Owl fitness and abundance and features of the forest system. The envirogram illustrates the relationship between Boreal Owl fitness and abundance and features of the forest system.

The evidence regarding roosting and foraging at a fine scale, Boreal Owl characteristics of mature forest stands suggests that level of stands will likely Boreal Owls.

Landscape Scale Habitat. Patterns of Boreal Owl landscape patterns is not direct evidence. Indirect evidence from America suggests that among forest habitats, observations of owls in landscapes dominated by those with mature spruce-fir (Larix sp.), Pseudotsuga (Pseudotsuga) or aspen (Populus) the greatest abundance (1992, 1993). In other forests that generally support Boreal Owls, ties in mature spruce-fir habitat.

More direct evidence suggests that landscape features influence Boreal Owl density in a portion of Scotch pine forest (Picea abies) and spruce-fir (Picea canadensis) quality of territories (nesting) increased (Koski et al. 1993). The suggestion that territories with high quality habitat was corroborated by high nesting frequency and clutch size.

Regional Scale Habitat. Broad geographic scale patterns of Boreal Owl distribution may also be influenced by landscape features.

RB Vole

BOREAL OWL MATING HABITAT IN THE NORTHWESTERN UNITED STATES

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ABSTRACT.—We examined boreal owl (*Aegolius funereus*) mating habitat in the Sierra Madre range of the Medicine Bow National Forest in Wyoming in the northwestern United States during 1992–93. In nocturnal surveys, we found 22 boreal owl singing locations which we compared to 68 random locations in the study area. Owls used stands dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) more often (77%) than stands of lodgepole pine (*Pinus contorta*). Stand size ranged from 0.2–122.8 ha though adjacent stand type (forest or opening) was not investigated. All boreal owls were found in areas with old forest characteristics including high basal areas of trees, tall snags, many large down logs, and a tall overstory canopy. Some boreal owls sang from old forest stands adjacent to clearcuts, one as close as 15 m. Older forests may provide nest holes for boreal owls which are obligate cavity nesters.

KEY WORDS: boreal owl; *Aegolius funereus*; mating habitat; old growth; Sierra Madre Forest; clearcut.

Habitat de apareamiento de *Aegolius funereus* en el noroeste de los Estados Unidos

RESUMEN.—Durante 1992 y 1993, examinamos el hábitat de apareamiento de *Aegolius funereus* en la Cordillera de Sierra Madre del Medicine Bow National Forest en Wyoming, al noroeste de los Estados Unidos. En recorridos nocturnos, encontramos 22 sitios de canto de este búho, los que comparamos con 68 sitios al azar en el área de estudio. Los búhos usaron más a menudo (77%) parches dominados por *Picea engelmannii* y *Abies lasiocarpa* que parches de *Pinus contorta*. El rango del tamaño del parche fue de 0.2 a 122.8 ha. Todos los búhos fueron encontrados en áreas con características de bosque antiguo, incluyendo grandes áreas basales de árboles, ramas espigadas, grandes troncos caídos y grandes sotobosques. Algunos individuos de esta especie se encuentran hasta alrededor de 15 m de claros de bosque. Antiguos bosques pueden proveer de sitios de nidificación para estos búhos que nidifican obligadamente en cavidades.

[Traducción de Ivan Lazo]

Boreal owl (*Aegolius funereus*) mating and nesting habitat is poorly understood in the U.S. because of their nocturnal behavior in remote forests. During their late winter mating season in the western states, boreal owls associate with older high-elevation forests generally composed of Engelmann spruce (*Picea engelmannii*, ES) and subalpine fir (*Abies lasiocarpa*, SA) (Webb 1982, Palmer 1986, Hayward et al. 1993). High elevation patches of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and quaking aspen (*Populus tremuloides*) are important when available (Hayward et al. 1993). These forest types also support the owl's primary prey, the southern red-backed vole (*Clethrionomys gapperi*) (Hayward et al. 1993).

During the mating season, male owls sing for a mate with a continuous high-pitched song that can easily be heard from 1.5 km and, on clear, cold nights, up to 3.5 km (Bondrup-Nielsen 1984). This allows an observer to locate owls without excessive intrusion. Owl singing locations indicate habitat use and represent potential breeding sites (Meehan 1980, Bondrup-Nielsen 1984, Hayward et al. 1993). Breeding sites vary by vegetation type but boreal owls are obligate cavity nesters (Mikkola 1983).

In this study, we sought to describe habitat used by boreal owls during the 1992–93 mating seasons. We compared owl singing locations with random habitat locations within the study area. The research also illustrates the distribution of boreal owl singing locations in a mosaic of forest patches comprised mainly of lodgepole pine (*Pinus contorta*,

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Boreal owl breeding season home ranges have been reported to vary between 240–352 ha for two birds in Colorado (Palmer 1986) and to average 1451 ± 552 ha in Idaho (Hayward et al. 1993).

At this scale, boreal owl singing locations were almost equally distributed by cover type into SF stands (55%) and LP stands (45%). This differed from plot level cover type designation (from cluster analysis) for three of the 16 stands used by singing boreal owls.

The mean stand size at the study area (6.9 ± 13.7 ha) differed from mean stand size at owl locations (35.5 ± 36.4 ha, $P = 0.0067$). Stands in the available habitat ranged in size from 0.005–122.8 ha; stands used for singing ranged from 0.17–122.8 ha.

Distance to Clearcuts. The 227 small clearcuts in the Coon Creek watershed have left 82% of the forest within 200 m of a clearcut. The maximum possible distance from a clearcut is 270 m (E. O'Doherty pers. comm.). Boreal owl singing locations did not differ in the distance to a clearcut from the random available habitat locations ($\chi^2 = 1.65$, $df = 1$, $P = 0.199$). The chi-square test of homogeneity tested the two categories of distance to a clearcut (<51 m, >51 m) for boreal owl singing locations ($N = 16$ in this watershed) and random available habitat sampling points ($N = 29$ in this watershed). Further, a t -test between the measured distances (<51 m) showed no difference ($P = 0.65$) in the mean distance to a clearcut between owl singing locations (29 ± 12.8 m) and the available habitat sampling points (31.7 ± 12.9 m) in the Coon Creek watershed. The closest "singing tree" to a clearcut was 15 m and the average distance was 27 ± 30 m.

DISCUSSION

13"
The majority of owl singing locations at the Blackhall Mountain study area were in the SF cover type with microhabitat structure typical of mature or old-growth forests (large downed logs, a high overstory canopy, tall snags, large ES trees, and small fir trees). Large snag (>39 cm dbh) density at owl singing locations, greater than in either the available habitat or other study areas in Colorado (Palmer 1986, Ryder et al. 1987) or Idaho (Hayward et al. 1993), increases the potential for suitable nest sites for boreal owls. Dense ES forests also offer protection from predators such as pine marten (*Martes martes*) (Korpimäki 1988) and larger birds of prey (Mikkola 1983). The singing locations

in LP cover types had large lodgepole trees instead of ES trees, as did boreal owl singing locations in LP stands on the Beaverhead National Forest in Idaho (Hayward et al. 1993). Hence, some LP stands appear to have adequate forest structure for boreal owls to use as singing sites.

Canopy height and large downed logs were identified as important differences between owl singing sites and random sites in both multivariate and univariate tests. Large downed logs are an important component of old-growth forests (Maser et al. 1979, Meslow et al. 1982) and were correlated with boreal owl mating habitat on our study area. Webb (1982) also described three of his five boreal owl locations in northern Colorado as having "much fallen timber." Although studies on boreal owl foraging sites did not report the log component directly, the highest numbers of foraging sites were in mature or older SF forests that support the owl's primary prey, the red-backed vole (Palmer 1986, Hayward et al. 1993). The old-growth locations used by boreal owls during the mating season at the Blackhall Mountain study area may also be used for foraging.

Microhabitat at owl singing locations indicated that SF cover types were used most often by boreal owls. Similarly, Palmer (1986) found a higher density of boreal owls in Colorado's high elevation SF though four other habitat types were available. Only in years with an abundance of boreal owls at his study area were lower elevation mixed forest habitat types used. He suggested that the SF is optimum habitat in the Cameron Pass area (Palmer 1986) 87 km south of the study area.

Hayward et al. (1993) found from surveys throughout the northern Rockies that a majority of boreal owl locations were in SF habitat types. In Idaho, the owls bred more often in mixed conifer and aspen habitats and, in the wilderness study site, did not nest in boxes hung in LP stands. At Blackhall Mountain, the aspen cover type was not available, and some LP stands were used for singing. Like some of the boreal owl singing sites in Colorado (Palmer 1986, 1987), sites used in Blackhall Mountain during mating season may be suboptimal. Without knowing the density and reproductive success of boreal owls at the Blackhall Mountain study area and in the surrounding habitat, inferences about the use of areas of lesser quality could not be made. Hayward et al. (1993) suggested that suboptimal habitat may still be important at a regional and metapopulation scale.

The discrepancy in cover-type designation between USFS maps and the cluster analysis for three of the 16 stands used by singing boreal owls is probably due to the difference in scale. This situation illustrates the importance of collecting habitat data on the ground rather than from a large-scale map.

The wide range of stand sizes used by singing boreal owls at Coon Creek suggests that even small stands provide forest structure to allow the owls to attempt breeding. However, adjacent stand conditions (clearcut, cover type, stand size, etc.) were not investigated though they may have had a significant influence. Also, the present and future degree of suitability of these small sites was unknown. Rosenberg and Raphael (1986) found that small patches of old-growth support forest-interior species, although their smallest stand measured 5 ha. In the long term, as the amount of habitat available is reduced, owl populations will decline (Hayward et al. 1993).

The choice of habitat made by boreal owls may be of ecological importance to their survival. Microhabitat selection may help avoid predation by larger owls. Food supply may be easier to obtain thereby conserving energy in this very harsh environment.

Boreal owls in the Coon Creek watershed sang in trees near clearcut edges. The "singing tree" and microhabitat data suggested that old-growth conditions are found near the edges of clearcuts. Owls may use edges for several other reasons. If the location was used for nesting prior to the clearcuts, it may continue to be used because of nest site tenacity by male boreal owls when suitable nest sites are scarce as in Sweden (Lundberg 1979) and western Finland (Korpimäki 1988). If clearcutting eliminated more suitable sites and packed owls into remaining forest, suboptimal locations may be used. Korpimäki (1987), for example, found that male boreal owls used nest holes just over 1 km from the edge. We speculate that stand structure is more important than any factor relating to edge. Boreal owl populations are associated with old growth characteristics including large, tall trees. Large downed logs are an indirect indicator of such stands and may also provide foraging sites for boreal owls.

Perhaps the most intriguing finding of this study is that the majority of the singing locations were in the watershed containing clearcuts. Korpimäki (1988) found that Tengmalm's owls in western Fin-

land preferred voles (*Microtus* sp.) that occupied clearcut areas where snow melted earlier than in woodlands. During breeding, which starts as the snow is melting, these owls mainly hunted in fields. He found that agricultural lands interspersed with productive ES forests lowered the variability of food supply which benefitted breeding owls. The mosaic of openings and forests provided several species of small mammals and therefore balanced the seasonal and year-to-year population fluctuations. Foraging boreal owls in Norway avoided clear-fellings that had higher prey densities than old-forest stands because the higher, denser vegetation made prey less accessible (Sonerud et al. 1986). Recent clearcuts in the Coon Creek watershed may provide greater prey availability for boreal owls at forest edges than in the undisturbed East Fork watershed. It is possible the owls have benefitted from some clearcutting in the short-term.

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PROCEEDINGS OF A SYMPOSIUM

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DEFINING ELK SECURITY: THE HILLIS PARADIGM

Pgs 38-43 1991

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.

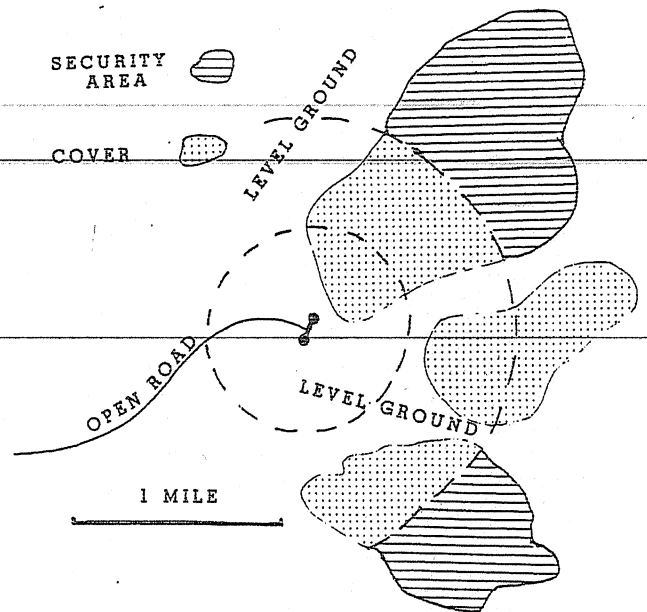


Figure 1. Sequoia-Brewster area, showing the relationship of security to an open road, recognizing the trailhead, level ground, and concentrated use. The one half mile zone was increased to 1 mile.

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

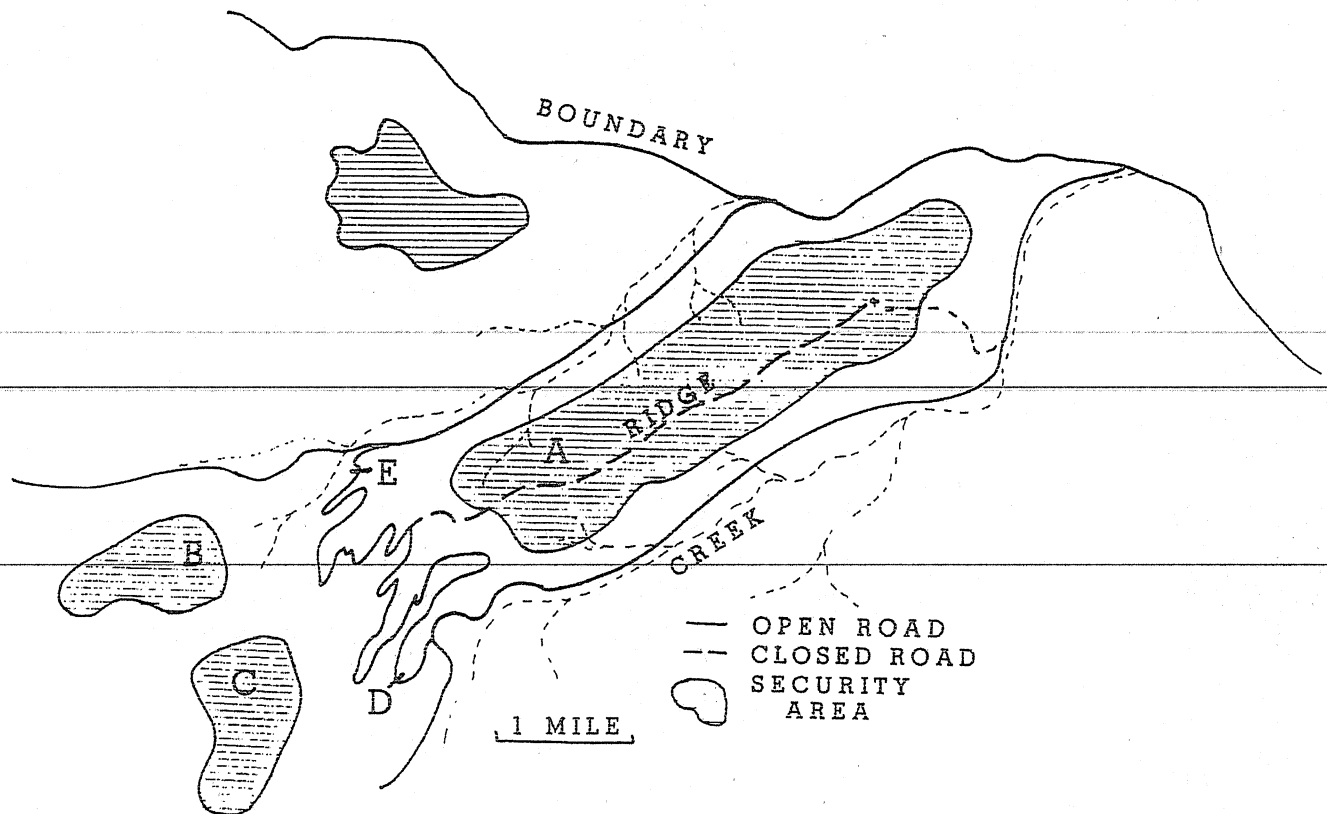


Figure 2. Tujo area, showing how security area A is affected by the ridgetop closed road. The proposed solution is to close the connecting road at points D and E.

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.

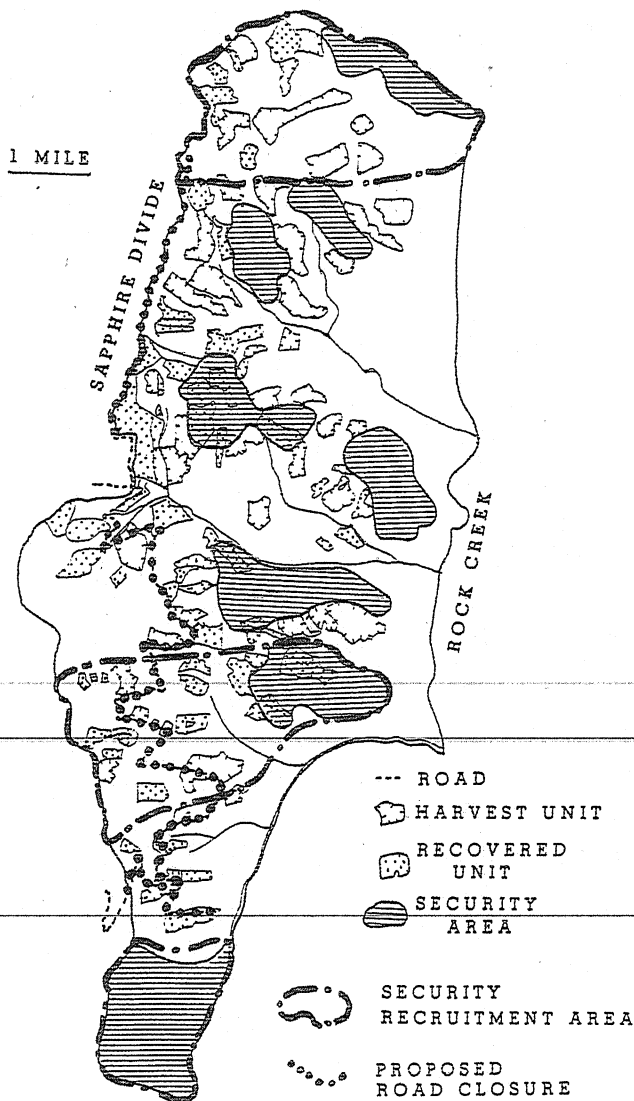


Figure 3. Sapphire Divide area, showing designated security recruitment areas and roads proposed for closure. Note how the past harvest pattern has fragmented cover.

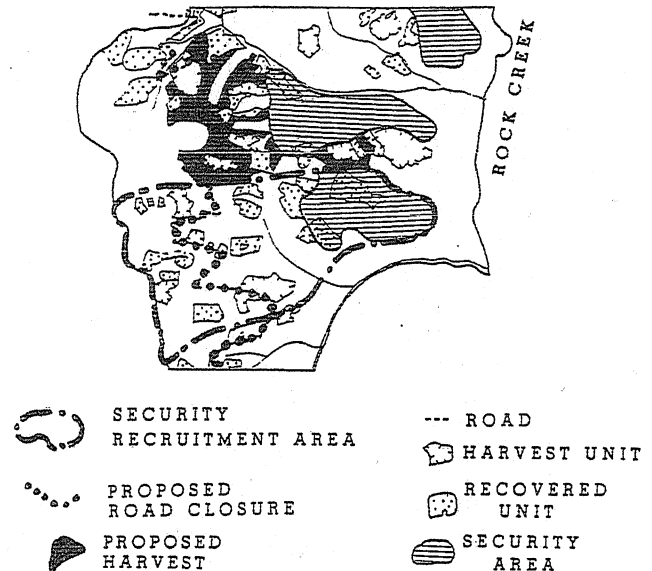


Figure 4. South Sapphire Divide area, showing a clustered timber harvest strategy designed to create a large block of future security. Note how proposed cutting units are adjacent to recovered harvest units.

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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2017a

HR = 55 km²
13,500
66% hares
740% CC

Received
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

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.

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 multivariate 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

$$11.1 \rightarrow 4.7 = -58\%$$

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

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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Table 1. Variables used in a priori habitat model building for northern and southern flying squirrels, eastern chipmunks, and red squirrels at site and landscape scales in logged and old hardwood and pine forest sites in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Scale	Species	No. of models	Variables ^a
Hardwood			
Site	Southern flying squirrel	15	Year, BA, Mast $\geq$ 25, Conifer, Declin $\geq$ 25
Landscape	Southern flying squirrel	15	LMast, LAverBA, LConifer
Site	Northern flying squirrel	15	CanClos, Conifer, Spruce $\geq$ 25, Snags, DWD $\geq$ 25
Landscape	Northern flying squirrel	6	LAverBA, LConifer, LSpruce
Site	Eastern chipmunk	15	Year, Conifer, Declin $\geq$ 25, Understory, DWD $\geq$ 25, DWDdc45
Landscape	Eastern chipmunk	4	LAverBA, LMast, LConifer
Site	Red squirrel	15	CanClos, Conifer, Spruce $\geq$ 25, Snags, DWD $\geq$ 25
Landscape	Red squirrel	8	LAverBA, LConifer, LSpruce
Pine			
Site	Southern flying squirrel	21	BA, Conifer, Hardwd, Hwd $\geq$ 25, Mast $\geq$ 25, Snags $\geq$ 25
Landscape	Southern flying squirrel	8	LAverBA, LMast, LMixed
Site	Northern flying squirrel	21	CanClos, Hwd $\geq$ 25, Spruce $\geq$ 25, Snags $\geq$ 25, DWD $\geq$ 25
Landscape	Northern flying squirrel	4	LAverBA, LSpruce, LAreaCut
Site	Eastern chipmunk	15	Year, Hardwd, Conifer, Snags $\geq$ 25, Hunderstory, DWDdc1–3
Landscape	Eastern chipmunk	4	LAverBA, LMast, LConifer
Site	Red squirrel	10	Year, Hwd $\geq$ 25, Spruce $\geq$ 25, Snags $\geq$ 25, DWD $\geq$ 25
Landscape	Red squirrel	9	LSpruce, LAreaCut, LMixed

^a See text for definition of habitat variables.

since the 1950s. Average forest age in the 3 logging histories (from FRI data) was 148, 142, and 135 years, respectively, and average basal area was 30.98 m²/ha (SE = 1.43), 18.96 m²/ha (SE = 1.16), and 20.65 m²/ha (SE = 0.82), respectively. In addition, within each logging history we attempted to systematically sample grids from a diverse array of mast and conifer compositions. We defined mast trees as those producing mast (both hard and soft mast; American beech, red oak [*Quercus rubra*], and black cherry [*Prunus serotina*]). Specifically, we selected approximately equal numbers of stands where the forest composition was 1) sugar maple-dominated, 2) mixed sugar maple-beech stands, or 3) mixed sugar maple-conifer stands. The dominant conifer species in hardwood stands was eastern hemlock, with smaller amounts of white spruce, balsam fir, and eastern white cedar (*Thuja occidentalis*).

In the eastern pinelands, we only sampled old-forest white pine stands and recent (3- to 10-yr-old) pine shelterwood cuts. Average FRI-based ages of both stand types was 100 years, and average basal areas were 30.68 m²/ha (SE = 1.28) and 20.01 m²/ha (SE = 1.79), respectively.

Sciurid Trapping

We sampled 10 grids in 2002, an additional 26 in 2003, and an additional 6 in 2004. We trapped all grids for 5 consecutive nights twice per summer, for a total of 10 trap-days/grid, with an interval of 4–7 weeks between trapping sessions. We attempted to sample recent cuts, old cuts, and old-forest sites equally in each trap session. For all grids, the average nearest neighbor distance between grids was 2.1 km (range: 0.6–13.6 km).

We used different trapping methodology in 2002 and in 2003–2004. In 2002, following Carey et al. (1991), we sampled each site using a 9 × 9 grid with 40-m spacing. We established 6 grids in hardwood stands (2 old forest, 2 recent cut, and 2 old cut), and 4 in white pine (2 old forest and 2 recent cut). We set 2 traps at every station, one attached to a

tree at 1.5 m in height and one on the ground. We placed tree traps on top of 2 large nails and secured them with an elastic cord. We set extra-large Sherman traps (10.2 × 11.4 × 38.1 cm) in the trees and standard-sized Sherman traps (5.1 × 6.4 × 22.9 cm) on the ground. We baited traps with a peanut butter and oats mixture and a slice of apple.

We modified this method in 2003–2004 for several reasons. First, we found that even within a treatment type, sciurid densities varied considerably among grids. Therefore, we increased replication of our trapping grids. In order to trap more grids, given a limited trap supply and limited person-power, we decreased the grid size. Second, because ground traps contributed little to captures of tree squirrels, we used only one extra-large Sherman tree trap per grid station. Finally, we changed our baiting regime due to extensive black bear (*Ursus americanus*) depredation: we used soaked, unshelled sunflower seeds and a slice of apple inside the trap, and peanut butter smeared on the tree near the trap door. In 2003, we live-trapped 18 grids in hardwood sites (6 old forest, 6 recent cut, and 6 old cut) and 8 in white pine sites (5 old forest and 3 recent cut). Twenty-three grids were small (4 × 9) with 40-m spacing and 3 were larger (either 6 × 11 or 8 × 9). We established the large grids in support of radiotelemetry studies (Holloway 2006). We live-trapped 6 sites in 2004, consisting of 2 old-forest white pine stands (4 × 9 grids), 2 recent shelterwood cuts (4 × 9 grids), and 2 old-forest hardwood grids (6 × 11 grids).

Habitat Measurements

Site-level measurements.—We used prism sweeps (basal area factor = 2) to quantify forest composition and structural characteristics at each of the 42 sites. In the sweeps, we measured all trees and snags with dbh above 10 cm and identified them to species. We made prism sweeps at 4–5 randomly selected stations/grid line for a total of 16–36 sweeps/grid, depending on grid size. We noted live trees as declining if more than one-half of the canopy showed signs

Table 4. The best 3 Akaike's Information Criterion adjusted for small sample size (AIC_c) models predicting densities for northern and southern flying squirrels, eastern chipmunks, and red squirrels at site and landscape scales in hardwood forest in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Species ^a	Model rank	Variables ^b	ΔAIC _c	w _i	r ²	P
Site scale						
Southern flying squirrel	1	Year, Snags, Conifer	0.00	0.27	0.48	0.001
	2	Year, Snags, Mast ≥ 25	0.18	0.25	0.48	0.001
	3	Year, Snags ^{c,d}	0.94	0.17	0.51	<0.001
Northern flying squirrel	1	CanClos	0.00	0.17	0.04	0.369
	2	Spruce ≥ 25	0.33	0.15	0.03	0.488
	3	Conifer	0.67	0.13	0.07	0.710
Eastern chipmunk	1	Year, DWDdc45, Declin ≥ 25 ^{c,d}	0.00	0.54	0.64	<0.001
	2	Year, DWDdc45	1.79	0.22	0.59	<0.001
	3	Year, DWDdc45, Conifer	4.36	0.06	0.58	<0.001
Red squirrel	1	Spruce ≥ 25, Snags ^d	0.00	0.27	0.49	0.003
	2	Spruce ≥ 25 ^c	0.45	0.22	0.37	0.004
	3	Snags	1.72	0.11	0.32	0.009
Landscape scale						
Southern flying squirrel	1	Year, Snags, Conifer, LAverBA	0.00	0.20	0.56	0.001
	2	Year, Snags, LMast ^{c,d}	0.05	0.20	0.58	<0.001
	3	Year, Snags, LAverBA	0.32	0.17	0.51	0.001
Northern flying squirrel	1	LAverBA ^{c,d}	0.00	0.35	0.24	0.023
	2	LAverBA, LSpruce	1.03	0.21	0.16	0.205
	3	LAverBA, LConifer	1.64	0.15	0.20	0.134
Eastern chipmunk	1	Year, DWDdc45, Declin ≥ 25, LConifer	0.00	0.48	0.69	<0.001
	2	Year, DWDdc45, Declin ≥ 25 ^{c,d}	1.29	0.25	0.64	<0.001
	3	Year, DWDdc45, Declin ≥ 25, LAverBA	1.79	0.20	0.66	<0.001
Red squirrel	1	Spruce ≥ 25, LConifer	0.00	0.15	0.49	0.003
	2	Spruce ≥ 25, Snags ^d	0.01	0.15	0.49	0.003
	3	Spruce ≥ 25, Snags, LSpruce	0.27	0.13	0.58	0.003

^a Models for southern flying squirrels and eastern chipmunks, and those for northern flying squirrels and red squirrels were developed using linear and logistic regression, respectively.

^b See text for definition of habitat variables.

^c Best model predicted by stepwise linear/logistic regression.

^d We give parameter estimates for this model in text.

Table 5. The best 3 Akaike's Information Criterion adjusted for small sample size (AIC_c) models predicting densities for northern and southern flying squirrels, eastern chipmunks, and red squirrels at the site and landscape scales in pine forest in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Species	Model rank	Variables ^a	ΔAIC _c	w _i	r ²	P
Site scale						
Southern flying squirrel	1	Hwd ≥ 25, Snags ≥ 25	0.00	0.32	0.53	0.014
	2	Mast ≥ 25 ^{b,c}	0.42	0.26	0.35	0.025
	3	Mast ≥ 25, Conifer	3.05	0.07	0.39	0.043
Northern flying squirrel	1	Spruce ≥ 25, Hwd ≥ 25, DWDdc13 ^{b,c}	0.00	0.53	0.75	<0.001
	2	Spruce ≥ 25, DWD ≥ 25	2.33	0.16	0.65	<0.001
	3	Spruce ≥ 25, Hwd ≥ 25	2.78	0.13	0.64	0.001
Eastern chipmunk	1	Year, Conifer ^{b,c}	0.00	0.30	0.55	0.002
	2	Year, Conifer, Hunderstory	1.02	0.18	0.60	0.003
	3	Year, Hunderstory	1.91	0.12	0.49	0.005
Red squirrel	1	Year, Spruce ≥ 25, DWDdc13	0.00	0.28	0.63	0.002
	2	Year, Snags ≥ 25 ^{b,c}	0.64	0.20	0.57	0.002
	3	Year, Spruce ≥ 25	1.29	0.15	0.56	0.002
Landscape scale						
Southern flying squirrel	1	Hwd ≥ 25, Snags ≥ 25	0.00	0.44	0.53	0.014
	2	Mast ≥ 25 ^{b,c}	0.42	0.36	0.35	0.025
	3	Mast ≥ 25, LAverBA	4.41	0.05	0.32	0.070
Northern flying squirrel	1	Spruce ≥ 25, Hwd ≥ 25, DWDdc13 ^{b,c}	0.00	0.79	0.75	<0.001
	2	Spruce ≥ 25, Hwd ≥ 25, DWDdc13, LMixed	4.33	0.09	0.74	0.001
	3	Spruce ≥ 25, Hwd ≥ 25, DWDdc13, LSpruce	5.12	0.06	0.73	0.001
Eastern chipmunk	1	Year, Conifer, LMast ^{b,c}	0.00	0.88	0.74	<0.001
	2	Year, Conifer	5.58	0.05	0.55	0.002
	3	Year, Conifer, LConifer	6.49	0.03	0.61	0.002
Red squirrel	1	Year, Snags ≥ 25, LAreaCut ^{b,c}	0.00	0.63	0.76	<0.001
	2	Year, Spruce ≥ 25, DWDdc13, LAreaCut	1.93	0.24	0.74	0.001
	3	Year, Spruce ≥ 25, DWDdc13	5.30	0.05	0.63	0.002

^a See text for definition of habitat variables.

^b Best model predicted by stepwise linear regression.

^c We give parameter estimates for this model in text.

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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.

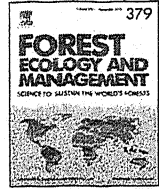
Additional keywords: Black-backed Woodpecker, conifer forest, ecological integrity, fire severity, mixed-severity fire, restoration, salvage logging, wildfire.

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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



Patterns of bird species occurrence in relation to anthropogenic and wildfire disturbance: Management implications

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ABSTRACT

We used a chronosequence approach to investigate the relationship between existing conditions of forested land that burned at some point between 1984 and 2014 in western Montana and the abundances of various bird species based on 7533 point-counts. Twelve of 68 bird species occurred significantly more frequently in burned mixed-conifer forest than in any of 13 unburned vegetation types, and most of them reached their greatest abundance in the severely burned portions of those forests. After restricting the analysis to conifer forest types only, 33 of 68 species (49%) were significantly more abundant in burned forest at some combination of time-since-fire and fire severity than in unburned conifer forest. One species, the black-backed woodpecker (*Picoides arcticus*), occurred nearly exclusively in severely and recently burned mixed-conifer forests. Its restricted distribution suggests that it must have evolved in the presence of those burned-forest conditions and, therefore, that it accurately reflects historical post-fire conditions that are critical to maintain on the landscape. This disturbance-dependent species was also affected strongly and negatively by both pre-fire and post-fire tree harvesting. Two important management implications follow directly from these findings: (1) the presence of the full complement of bird species in a landscape cannot be maintained through land management that either suppresses fire or acts to reduce overall fire severity through widespread forest thinning or through the application of homogeneous, low-severity, prescribed burning across the broader landscape—only severe fire can produce the variety of post-fire conditions used by species that are nowhere more abundant than in burned forests; and (2) the presence of many species (especially those most specialized to use burned forest conditions) is incompatible with both pre-fire and post-fire timber harvesting. To maintain the ecological integrity of disturbance-dependent mixed-conifer forest systems, land managers must, therefore, use strategic landscape planning to harvest trees while still retaining both an abundance of minimally disturbed, unburned, mature-forest conditions and an abundance of severely burned forest conditions that emerge from natural fire disturbance events.

1. Introduction

Fire is the most widespread and important agent of natural disturbance in the Rocky Mountains, where 80–90% of all forest types support either a mixed- or high-severity fire regime (Baker, 2009; DellaSala et al., 2015). It has been noted that within the Northern Rocky Mountains, "...a high percentage of vegetation, within all forest zones, is at one stage or another of succession following past fires" (Habeck and Mutch, 1973); indeed, climax forests that have escaped fire or that have experienced only low-severity understory fires are rare in the northern Rockies. The ecological importance of fire as a disturbance agent can be readily exposed through study of one of the most effective biological indicator groups—birds. Two decades ago, Hutto

(1995) published the first comparison of published bird survey data collected from a broad range of unburned vegetation types with his own survey data collected from burned conifer forests. The results were striking. Not only were nearly 100 bird species detected in burned forests, but comparative data also suggested that 15 of those species were nowhere more abundant than in burned forest conditions, and a few (most notably, the black-backed woodpecker, *Picoides arcticus*) were nearly restricted in their distribution to burned forests.

Research over the subsequent two decades has only reinforced that original finding. For example, the same patterns emerged from the use of more than 10,000 point-count surveys conducted across a comprehensive range of vegetation types (Hutto, 2008). Fire scientists have also come to understand that an organism's response to fire depends on

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Toward a more ecologically informed view of severe forest fires

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Abstract. We use the historical presence of high-severity fire patches in mixed-conifer forests of the western United States to make several points that we hope will encourage development of a more ecologically informed view of severe wildland fire effects. First, many plant and animal species use, and have sometimes evolved to depend on, severely burned forest conditions for their persistence. Second, evidence from fire history studies also suggests that a complex mosaic of severely burned conifer patches was common historically in the West. Third, to maintain ecological integrity in forests born of mixed-severity fire, land managers will have to accept some severe fire and maintain the integrity of its aftermath. Lastly, public education messages surrounding fire could be modified so that people better understand and support management designed to maintain ecologically appropriate sizes and distributions of severe fire and the complex early-seral forest conditions it creates.

Key words: early succession; ecological integrity; ecological system; fire management; fire regime; forest resilience; forest restoration; severe fire; wildfire.

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INTRODUCTION

The spatiotemporal expression of fire events over time in any landscape produces a “fire regime” that influences ecosystem dynamics in that area (Heinselman 1981, Kilgore 1981). Even though the various characteristics of a fire regime (Table 1) are continuous in nature, the traditional approach in representing this variation has been to create a small number of discontinuous categories. Fire regimes in western North America, for example, are often classified into as few as three categories: (1) low-severity, (2) mixed-severity, and

(3) high-severity or stand-replacement (Agee 1998, Brown 2000). Our attempt to categorize fire regimes is “. . . an oversimplification...for the convenience of humans” (Sugihara et al. 2006; p. 62), and has had the unfortunate consequence of minimizing rather than emphasizing variation in fire behavior and fire outcomes among vegetation types and across spatial scales (Morgan et al. 2014). In reality, relatively few forest types fit entirely within either of the two extremes—the low-severity (e.g., some interior ponderosa pine) or the stand-replacement (e.g., Rocky Mountain lodgepole pine) categories. Instead, as a simple analysis

Table 1. Characteristics or descriptors often used to describe disturbance regimes (from Keane 2013).

Disturbance Characteristic	Description	Example
Agent	Factor causing the disturbance	Fire is an agent that can kill trees
Source, Cause	Origin of the agent	Lightning is a source for wildland fire
Frequency	How often the disturbance occurs or its return time	Years since last fire (scale dependent)
Intensity	A description of the magnitude of the disturbance agent	Wildland fire heat output
Severity	The level of impact of the disturbance on the environment	Fuel consumption in wildland fires; change in biomass
Size	Spatial extent of the disturbance	Tree kill can occur in small patches or across entire landscapes
Pattern	Patch size distribution of disturbance effects; spatial heterogeneity of disturbance effects	Fire can burn large regions but weather and fuels can influence fire intensity and therefore the patchwork of tree mortality
Seasonality	Time of year of that disturbance occurs	Spring burn vs. fall burn
Duration	Length of time of that disturbances occur	Fires can burn for a day or for an entire summer
Interactions	Disturbance types may interact with each other, or with climate, vegetation and other landscape characteristics	Mountain pine beetles may create fuel complexes that facilitate or exclude wildland fire
Variability	The spatial and temporal variability of the above factors	Each of the above characteristics has variation associated with it

using LANDFIRE data (Rollins 2009, <<http://www.landfire.gov>>) reveals, roughly 85% of all forested lands within the western US fit within the mixed-severity category, which includes proportions of low-, moderate-, and high-severity (lethal to more than 70% of all trees) fire that vary widely across vegetation types and biophysical settings.

Agee (1993) captured the essence of this important idea in a graph depicting the proportion of low-, moderate-, and high-severity fire across the range of fire regimes (Fig. 1). Note that change from one fire regime to the next (movement along the *x*-axis) is accompanied not by the sudden appearance of a different fire severity, but by continuous changes in the proportions of each fire severity category. Thus, fire regimes blend imperceptibly into one another. More importantly, except for the two end points on the graph where the proportion of high-severity fire would be either 0% or 100%, most fire regimes consist of a mix of fire severities so, technically speaking, they fit best within a mixed-severity regime (Fig. 2). It is not the presence of a particular fire severity, but the proportion (and, presumably, the distribution and patch sizes) of each severity component that distinguishes regimes. Indeed, empirical

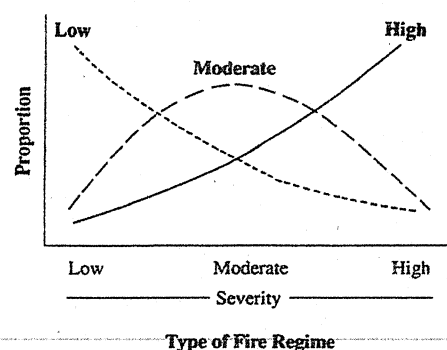


Fig. 1. This graph (from Agee 1993) illustrates that fire regimes are not characterized by the presence of only one kind of fire. Rather, it is the relative frequency of low-, moderate-, and high-severity fire in an average burn that varies among fire regimes.

data drawn from recent fires across the western United States between 1984 and 2008 (Fig. 3) reveal this continuous variation in proportions of different fire severities among fires. Thus, a more continuous view of fire regimes might be a better way to appreciate the infinite variability in fire behavior among forest types and geographic locations, and it might also promote a greater appreciation of severe fire as an integral

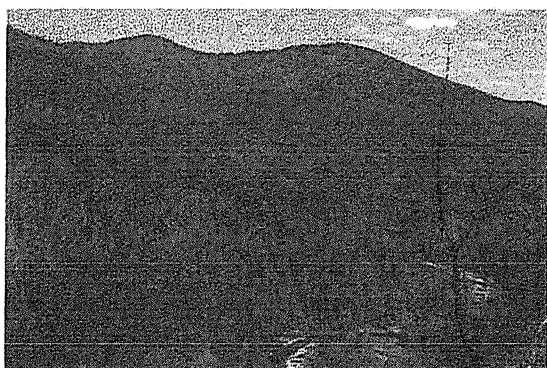


Fig. 2. Mixed-severity fires (fires that leave recognizable patches of low-severity, medium-severity, and high-severity effects) typify the majority of mixed-conifer forest systems in the western United States. The brown-needled and blackened areas harbor unique sets of plant and animal species found in no other forest conditions. This photograph of the North Fork of the Blackfoot River was taken 10 months after the 1988 Canyon Creek fire in Montana. Many fire-dependent plant and animal species were present in the more severely burned areas until they were helicopter logged, suggesting that unburned forests might be a better alternative for timber harvest.

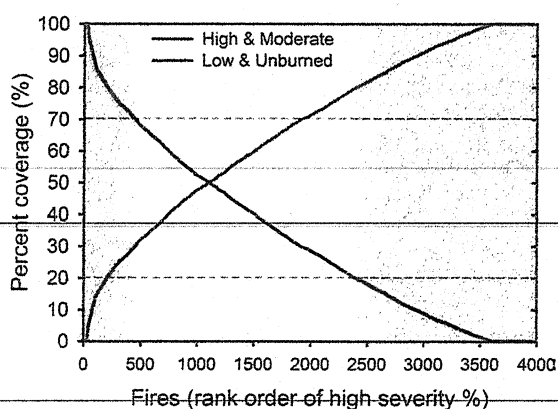


Fig. 3. The percent area within a fire perimeter that burned at low (green line) and at moderate to high (red line) severity is shown for a series of 3696 fires that burned in the western United States between 1984 and 2008 (after Belote 2015). The figure shows that the proportions of each severity category are continuously variable and that high-severity fire is a natural part of most forest fires in the West.

part of mixed- and high-severity conifer forest fire regimes.

Accordingly, we highlight the need for better information on the historical patterns and abundances of high-severity patches in different forest types. This is an important discussion because, even though our National Cohesive Wildland Fire Management Strategy (Wildland Fire Executive Council 2014) acknowledges that many fire regimes exist and that management needs to accommodate that variation and the variety of habitat such variation produces, contemporary fire management is focused heavily on the exclusion (prevention and suppression, collectively) or mitigation of severe fire. When either of those fails, management efforts seem to shift toward speeding the “recovery” of the forest after severe fire. With respect to the latter, there are repeated attempts to introduce legislation designed to expedite logging after fire (salvage logging). Although the removal of dead trees is justified near roads and structures for safety reasons, and although postfire logging can capture economic value of wood that would otherwise be lost, such logging has been shown to carry significant ecological costs (Hutto 2006, Lindenmayer and Noss 2006, Swanson et al. 2011, Lindenmayer and Cunningham 2013, DellaSala et al. 2015). The ecological benefits and necessity of severe fire (and its aftermath) has widespread implications for the flora and fauna that depend on the presence of burned forest conditions. Ecologically sound fire management includes land management designed to ensure the maintenance of ecologically appropriate mixes of fire severities within the forested landscapes of western North America while protecting homes and lives at the same time (Perry et al. 2011). An ecologically informed view of severe fire requires recognition that it is a natural component of many western conifer forests (Heinselman 1981, Arno 2000). Moreover, the severe-fire component must have been large enough and frequent enough to have favored the evolution of specialization by various plant and animal species to conditions that occur in the aftermath of severe fire. We offer the following points in an effort to better recognize and include severe fire as an integral part of fire management in mixed-conifer forest systems:

SEVERELY BURNED FORESTS CREATE
BIOLOGICALLY UNIQUE CONDITIONS THAT
CANNOT BE CREATED BY OTHER KINDS OF
DISTURBANCES OR THROUGH ARTIFICIAL MEANS

Patterns in the habitat associations of plant and animal species can provide definitive evidence that severe fire plays an essential role in the ecology of mixed-conifer forests (Hutto et al. 2008). Specifically, if a plant or animal species occurs only in burned forest conditions created by severe fire events, then it cannot be using burned forest conditions merely opportunistically. Instead, the species must have evolved to depend on such conditions because it occurs rarely, if ever, in unburned habitat (Swanson et al. 2011, DellaSala et al. 2014). For example, some moss and lichen species are relatively restricted to severely burned forest conditions (Ahlgren and Ahlgren 1960), as are the fire morel mushroom (*Morchella elata*) and Bicknell's geranium (*Geranium bicknellii*) in forests throughout the West (Heinselman 1981, Pilz et al. 2004). The black-backed woodpecker (*Picoides arcticus*) is emblematic of a species that is relatively restricted to early successional conditions created by high-severity fire (Hutto 1995, Dixon and Saab 2000, Hoyt and Hannon 2002). Black-backed woodpeckers are attracted to postwildfire conditions because of the abundance of larvae of a number of wood-boring beetle species that are attracted to the fire-killed trees (Murphy and Lehnhausen 1998, Rota et al. 2015). Several of these beetle species are themselves relatively restricted to recently burned forests (Saint-Germain et al. 2004a,b, Boucher et al. 2012). Importantly, black-backed woodpeckers are significantly more likely to occur in the more severely burned portions of a mixed-severity fire (Hutto 2008, Latif et al. 2013). Although black-backed woodpeckers are known to occur outside severely burned forests on rare occasions, detailed study of survival and reproductive success shows that they exhibit growing populations only in forests recently burned by summer wildfires (Rota et al. 2014). The adaptations of thick bark, branch shedding, and serotiny in *Pinus* are thought to have evolved in response to a period of more intense crown fires in the mid-Cretaceous (He et al. 2012), and those adaptations also

reflect the severe-fire backdrop against which pine, Douglas-fir, and larch are thought to thrive.

Many additional animal species, while not as narrowly restricted to burned forest conditions, clearly benefit from the burned forest conditions created by severe fires in mixed-conifer forests throughout the West (Hutto et al. 2015). For example, nest survival of white-headed woodpeckers is significantly higher in burned (wildfire) compared to unburned forest (Hollenbeck et al. 2011, Lorenz et al. 2015). In aquatic systems, severe fire events can rejuvenate stream habitats by causing large amounts of gravel, cobble, woody debris, and nutrients to be imported, resulting in increased production and aquatic insect emergence rates (Benda et al. 2003, Burton 2005, Malison and Baxter 2010, Ryan et al. 2011, Jackson et al. 2015). These changes can, in turn, affect food web dynamics in a way that results in higher growth rates in young trout, including young coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) (Heck 2007) and rainbow trout (*Oncorhynchus mykiss*) (Rosenberger et al. 2011). Indeed, nonnative fish populations declined and native trout densities increased 3 yr after a severe fire in the Bitterroot River watershed, Montana, indicating that severe fire may help ensure ecological integrity of some western streams (Sestrich et al. 2011). In addition, native amphibians such as boreal toads (*Bufo boreas*) thrive in areas that burn severely (Dunham et al. 2007, Hossack and Corn 2007) and use severely burned areas more than expected due to chance (Hossack and Corn 2007, Guscio et al. 2008), as do some bat species (Buchalski et al. 2013).

These strong associations between organisms and severely burned forest patches suggests that many plant and animal species have evolved to rely on recurring severe wildfire events, and further indicates that severe fire events are a natural and important part of the fire regimes associated with many western mixed-conifer forest types. In other words, if one or more species occupy severely burned forests to the exclusion of other forest types (and if they do not tend to occupy forests disturbed through artificial means), then a severely burned forest would have to be considered natural, and would necessarily lie within the historical range of variation (Hutto et al. 2008). Moreover, a more intimate understanding

of the biology of those plants and animals (e.g., knowledge of dispersal processes and patterns, foraging ecology, home-range sizes) can provide insight into the historical spatial scales at which severe fire operated across the broader landscape.

FIRE HISTORY STUDIES SUGGEST THAT SEVERE FIRE IS AN INTEGRAL COMPONENT OF MOST FIRE REGIMES

In addition to the definitive evidence provided above, a growing body of fire history information points to the same conclusion—severe fire was historically, and is currently, an important component of many western conifer forest systems. At one end of the fire regime spectrum, conifer forests in the warmer, drier geographic areas in western North America are commonly characterized by frequent, low-severity fires that killed primarily juvenile trees historically, resulting in the maintenance of open pine forests with low densities of mature trees (Covington and Moore 1994a,b). Nevertheless, mixed and stand-replacement fires were possible even in these forest types after long inter-fire intervals, such as after an especially cold, wet period similar to what occurred during the Little Ice Age (Brown et al. 1999, Sherriff and Veblen 2007, Williams and Baker 2012, Odion et al. 2014, Hanson et al. 2015). At the other end of the fire regime spectrum, cooler, moister forest types, such as lodgepole pine forests, support fire regimes dominated by severe fire events (Brown and Smith 2000), although mixed- and low-severity fires are known to occur in these types as well (Barrett et al. 1991).

Between these two extremes lie the vast majority of mixed-conifer forest types in western North America. These include everything from the xeric, low-elevation, mixed ponderosa pine and Douglas-fir forest types to mesic, high-elevation, spruce-fir forest types. Unlike the forest types that are dominated by either the absence or presence of severe fire, mixed-conifer forests are best characterized by fire regimes of variable, or mixed severity (see Baker 2009: fig. 7.1), which means that the presence of sizable proportions of the three classes of fire severity characterize the fires that burn in those forest systems (Sherriff and Veblen 2006, 2007, Baker et al. 2007, Hessburg et al. 2007, Klenner et al. 2008, Perry

et al. 2011, Schoennagel et al. 2011). Importantly, extreme weather (e.g., high temperature, low humidity, high wind speed) rather than quantity of woody fuels often exerts the greatest influence on fire severity and extent across that broad range of mixed-conifer forest types (Johnson et al. 2003, Schoennagel et al. 2004, Lydersen et al. 2014, Williams et al. 2015). This means that, in contrast with the situation in low-elevation or xeric-type ponderosa pine forests in some areas of the southwestern United States (Keane et al. 2008), the amount of high-severity fire in other mixed-conifer forest types is less likely to have departed significantly from historical ranges of variability, even though those forests may have experienced measurable twentieth century changes in fuels due to fire exclusion, timber harvest, and cattle grazing (e.g., Baker et al. 2007, Dillon et al. 2011, Marlon et al. 2012, Miller et al. 2012, Odion et al. 2014, Sherriff et al. 2014). We recognize the lack of relevant historical information on landscape-level distributions and spatial scales of different classes of fire severity for many forest types and regions, but severely burned forest patches have probably always occurred naturally, even in pure ponderosa pine forests of the Southwest, as Cooper (1961) and Weaver (1943) described long ago. We also know that, at least throughout the northern half of the western United States, the extent of severe-fire patches must have been both substantial enough in area and frequent enough to support those plant (e.g., lodgepole pine) and animal (e.g., wood-boring beetle and woodpecker) species that evolved to depend on severe fire itself or on the resulting severely burned forest conditions.

MAINTAINING ECOLOGICAL INTEGRITY MEANS ACCOMMODATING A BROAD SPECTRUM OF FIRE SEVERITIES, INCLUDING SEVERE FIRE AND ITS AFTERMATH, IN MOST MIXED-CONIFER FORESTS

We have now established two important facts: severe fire (moderate-to-high burn severity) is a natural agent of disturbance in many mixed-conifer forest types, and such fire is thought to be ecologically necessary for the presence or success of many plant and animal species. These two facts make it clear that management to maintain the ecological integrity of any ecosystem that harbors species that depend on severe fire

as a disturbance agent will have to integrate severe fire and its effects into management goals. Moreover, if we better considered distribution patterns, home range sizes, movement patterns, and other animal adaptations that reflect the environment within which they evolved (e.g., Hutto et al. 2008), we could gain considerable insight into historical spatial scales under which severe fire operated as well. We are not questioning or attempting to discredit the evidence that some forest systems were historically dominated by low-severity fire; rather, we are encouraging land managers to also pay close attention to maintaining amounts and distributions of higher severity fire consistent with ecological integrity in our western mixed-conifer forests. The current science, management, and policy challenge for ecosystem managers is to estimate and incorporate amounts of low-, moderate-, and high-severity fire in a manner that maintains ecological integrity (Hessburg et al. 2007, Perry et al. 2011, Baker 2015).

While many fire ecologists understand the importance of more severe fire in forest ecosystems, politicians and the public at large have yet to reach the same understanding. Recent increases in the amount of forested area burned by wildfire over the past three decades in western North American forests (Westerling et al. 2006, Dennison et al. 2014) signaling what many believe to be the emergence of a new age of megafires (Attiwill and Binkley 2013), has created increased movement toward pre and postfire land management activities designed to reduce fire severity, mimic fire effects without the use of fire, or speed the recovery of a forest after fire. These activities may provide some societal benefits, but they can have real costs in terms of the way they negatively affect the ecological integrity of mixed-conifer forests born of mixed-severity fire. Removed from locations that pose a clear and immediate threat to human lives and property, the ecological costs associated with forest thinning may outweigh stated benefits by large margins. We highlight two types of land management (beyond fire suppression itself) that can have significant negative effects on fire-dependent species and, therefore, can interfere with our ability to maintain the ecological integrity of fire-dependent conifer forests: prefire fuel treatments and postfire salvage logging.

Prefire harvest treatments

We know a great deal about the effects of fuel treatments and restoration harvests on forest structure and vegetation recovery, but we know little about the ecological effects of such treatments on the prefire responses of most plant and animal species, and virtually nothing about postfire responses of the most fire-dependent plant and animal species after a treatment subsequently burns in a wildfire. This is because such treatments are rarely accompanied by "ecological effects monitoring," which, in contrast with implementation monitoring (evaluating whether a management activity was implemented) and effectiveness monitoring (evaluating whether the management activity achieved the stated goal), is specifically designed to address whether there are unforeseen negative ecological consequences of a management treatment (Hutto and Belote 2013).

Fuel treatments designed to restore fire-prone ecosystems should do so in the proper fire regime context; more specifically, they should produce appropriate postfire plant and animal responses when fire returns to the forest. Thus, treatments appropriate for dry forests that were historically maintained by a low-severity fire regime may be inappropriate for forests maintained by a mixed-severity fire regime. One serious negative consequence of canopy fuel reduction in forests that evolved with mixed-severity fire could be that fire-dependent species requiring high densities of large standing-dead trees created by the severe-fire component may not recruit after a subsequent fire. For example, the fire-dependent black-backed woodpecker was found to be even less abundant in mixed-conifer forests that were thinned before fire than in the same forest types logged after fire, even though the two pathways support similar standing dead tree densities. This is probably because birds rarely colonize thinned forests that burn, but they still make the best of a bad situation when trees are removed after they have already colonized a densely stocked, severely burned forest (Hutto 2008). Recent research on postfire soil conditions shows that soil C and N response following wildfire also depends on whether there have been fuel

treatments, so the assessment of fuel treatment effects needs to include postfire response and not simply postharvest response (Homann et al. 2015). It has been suggested (e.g., Franklin and Johnson 2014) that variable-retention harvests could be designed to emulate early-seral conditions following natural disturbance events in forests born of mixed-severity fire, thereby avoiding the negative consequences associated with other tree harvesting methods. Unfortunately, that strategy is unlikely to satisfy the needs of those fire-dependent animal species that require high densities of fire-killed trees immediately following severe fire (Schieck and Song 2006, Hutto 2008, Reidy et al. 2014).

Postfire salvage logging

Salvage logging after fire is intended to recover economic value of timber that would otherwise be lost, to ensure human safety, and to reduce the risk of future fires. Unfortunately, salvage harvesting activities undermine the ecosystem benefits associated with fire (Lindenmayer et al. 2004, Lindenmayer and Noss 2006, Swanson et al. 2011). For example, postfire salvage logging removes dead, dying, or weakened trees, but those are precisely the resources that provide nest sites and an abundance of food in the form of beetle larvae and bark surface insects (Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Saab et al. 2007, 2009, Cahall and Hayes 2009). No fire-dependent bird species has ever been shown to benefit from salvage logging (Hutto 2006, Hanson and North 2008). The ecological effects of salvage logging on aquatic ecosystems are also largely negative (Karr et al. 2004). In fact, the demonstrated negative ecological effects associated with postfire salvage logging are probably the most consistent and dramatic of any wildlife management effects ever documented for any kind of forest management activity (Hutto 2006). Therefore, because the National Forest Management Act and other legal mandates require public land managers to maintain the integrity of the larger ecological system, burned forests should perhaps be given special consideration compared with green-tree forests. Specifically, they could receive a low priority ranking when it comes to timber harvest

decisions (with the obvious exception of small harvests associated with roads and other areas where safety or infrastructure are legitimate concerns). Timber can be harvested from many green-tree forests in a manner that imposes relatively little ecological cost in comparison with the costs associated with logging in burned forest (Lindenmayer and Cunningham 2013).

HOW DO WE MOVE TOWARD A MORE ECOLOGICALLY INFORMED VIEW OF FOREST FIRES?

The ecological costs associated with some of the more commonly employed pre and postfire management activities in the western United States probably increase substantially as one moves from the low-elevation or xeric ponderosa pine or woodland forest types, where trees were widely spaced and severe fire historically played a spatially restricted role, to the broad array of more densely stocked mixed-conifer forest types, where severe fire historically played a major role. Therefore, a thorough understanding of the historical fire regime associated with any particular vegetation type or land area (as determined from multiple lines of evidence concerning regionally specific fire history) is critically important for land managers who concern themselves with the issues of wildfire risk, ecological restoration, or maintenance of the diversity of native species (Schoennagel and Nelson 2011). More specifically, quantification of appropriate fire rotations and proportions of low-, moderate-, and high-severity fire for any given forest landscape is critical for enlightened land management. For example, in some xeric ponderosa pine forest types, ecosystem restoration activities designed to decrease the severity of wildfire may be ecologically appropriate. The same management activities are not likely to be ecologically appropriate in many mixed-conifer forests, however, because key indicator species evolved to depend on significant amounts of severe fire in those forest types (Schoennagel et al. 2004, Hutto 2008, Klenner et al. 2008, Baker 2012, 2015, Williams and Baker 2012, Odion et al. 2014).

Land and fire managers are now facing future fires that many hypothesize will become larger and contain larger proportions of more severely

burned patches under warming climate conditions (Rocca et al. 2014). Problems associated with climate change, however, must be solved through efforts directed toward the causes of climate change and not toward the symptoms of climate change. Any perceived problem with future changes in fire behavior cannot be solved by redoubling our effort to treat this particular climate change symptom by installing widespread fuel treatments that do nothing to stop the warming trend, and do little to reduce the extent or severity of weather-driven fires (Gedalof et al. 2005). Therefore, fuel management efforts to reduce undesirable effects of wildfires outside the xeric ponderosa pine forest types could be more strategically directed toward creating fire-safe communities (Calkin et al. 2014, Kennedy and Johnson 2014). A management emphasis directed toward altering conditions in and immediately adjacent to human communities is very different from an emphasis directed toward treating massive amounts of fuel on more remote public lands. Fuel treatment efforts more distant from human communities may carry the negative ecological consequences we outlined earlier and do little to stop or mitigate the effects of fires that are increasingly weather driven (Rhodes and Baker 2008, Franklin et al. 2014, Moritz et al. 2014, Odion et al. 2014).

Public land managers face significant challenges balancing the threats posed by severe fire with legal mandates to conserve wildlife habitat for plant and animal species that are positively associated with recently burned forests. Nevertheless, land managers who wish to maintain biodiversity must find a way to embrace a fire-use plan that allows for the presence of all fire severities in places where a historical mixed-severity fire regime creates conditions needed by native species while protecting homes and lives at the same time. This balancing act can be best performed by managing fire along a continuum that spans from aggressive prevention and suppression near designated human settlement areas to active "ecological fire management" (Ingalsbee 2015) in places farther removed from such areas. This could not only save considerable dollars in fire-fighting by restricting such activity to near settlements (Ingalsbee and Raja 2015), but it would serve to retain (in the absence of salvage logging, of course) the ecologically important

disturbance process over most of our public land while at the same time reducing the potential for firefighter fatalities (Moritz et al. 2014). Severe fire is not ecologically appropriate everywhere, of course, but the potential ecological costs associated with prefire fuels reduction, fire suppression, and postfire harvest activity in forests born of mixed-severity fire need to be considered much more seriously if we want to maintain those species and processes that occur only where dense, mature forests are periodically allowed to burn severely, as they have for millennia.

Another integral part of moving toward an ecologically informed perspective of forest fire involves getting the public, politicians, and policy-makers to better recognize and appreciate the critical role that severe fire plays in many forest systems. This has been difficult, and this difficulty has been exacerbated by public messages about severe fire that are uniformly negative. Progress toward allowing fires to burn is difficult unless the public begins to receive a message that differs markedly from the message that Smokey the Bear is sending them now. Fires in our wildlands are fundamentally natural and beneficial, so we must learn to live in a way that allows naturally occurring fires, including severe fires, to burn while minimizing risk to human property and lives (Calkin et al. 2014). That is a vastly different message from one that says severe fires are fundamentally bad and that we have to do everything in our power to prevent and suppress them, or from one that says severely burned forests are places where we should expedite efforts to capture residual economic value through "salvage" logging. We challenge ecologists and managers to pay greater attention to the degree of variation in fire regimes within mixed-conifer forests and to recognize that prefire thinning and postfire "restoration" activities may not always be compatible with maintenance of the ecological integrity of conifer forests that depend on complex mixed-severity fire disturbance.

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Management Guide to Ecosystem Restoration Treatments: Whitebark Pine Forests of the Northern Rocky Mountains, U.S.A.

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Russell A. Parsons



United States Department of Agriculture
Forest Service



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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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Subject: Great Gray owls in Tetons logging impacts them.
From: George Wuerthner (gwuerthner@gmail.com)
To: stonefly@olypen.com;
Bcc: sjjohnsonkoa@yahoo.com;
Date: Wednesday, July 31, 2013 10:19 PM

Jackson Hole News & Guide

Environment

Biologists track owls to save homes from logging
Great grays fitted with GPS backpacks to learn about habits, numbers.

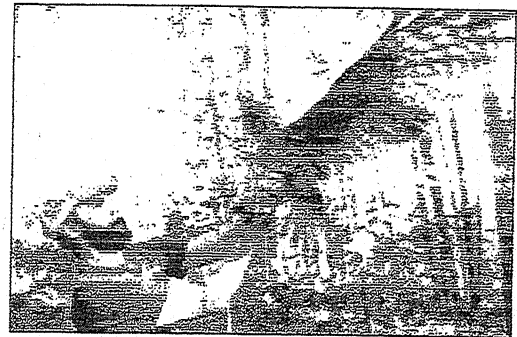
*By Mike Koshmrl, Jackson Hole, Wyo.
July 31, 2013*

Perched partway up a twisted pine, a great gray owl stared at a white mouse that had nowhere to run.

The mouse, tethered to the ground by an alligator clip, was planted by Craighead Beringia South biologists hoping to catch the female *Strix nebulosa*, which sat nearby panting. It was an easy meal, and the great gray had a clear line of sight on the critter, but she seemed not to give a hoot.

"Right when we arrived, she fed the fledgling a vole," said Beth Mendelsohn, who'd been tracking the owl since sunup. "This bird seems a little more spooky than most."

Mendelsohn, along with Katherine Gura and Bryan Bedrosian, had hoped to net and then fix a GPS-equipped backpack to the great gray. The team had managed to fix backpacks to five great grays this summer.



Craighead Beringia South biologist Bryan Bedrosian lets a captured gray owl spread its wings to allow a newly-attached tracking device to work into its feathers near Red Top Meadows. Bedrosian has been putting transmitters and ID bands on several owls in order to study the birds' home range.
BRADLY J. BONER / NEWS&GUIDE

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These are some of the first electronically tracked owls in the world, Bedrosian said. GPS trackers are usually solar-powered, and that's an issue because owls are most active at night.

The owl-catching crew came up empty-handed. The female, which was caring for a lone offspring, saw through the biologists' ploy.

"Some birds are like, 'yeah, nice try,'" Bedrosian, Beringia South's avian program director, said after giving up.

Beringia South, based in Kelly, is in the middle of the first great gray owl research project in Jackson

<http://us-mg4.mail.yahoo.com/neo/launch?.rand=akhhc7k7lql14>

8/7/2013

Hole in two decades. Biologists Susan Patla, with the Wyoming Game and Fish Department, and Kerry Murphy, with the Bridger-Teton National Forest, are collaborators. Funds have come from a state of Wyoming wildlife grant, the Community Foundation of Jackson Hole, Four Seasons Hotel and Resorts and Ecotour Adventures.

Locally, little is known about the species. Numbers, home ranges — it's all unknown territory, Bedrosian said.

What is known is that there aren't many great grays.

"We found very few owls," Bedrosian said, recalling a winter of combing the mountains from Grand Teton National Park to the Snake River. "There just isn't that many nests."

Meanwhile, the Teton to Snake Fuels Management Project, a wildfire reduction plan that will thin critical old-growth habitat, looms. Cuts, thinning and limbing is proposed in some of the birds' prime range in the Bridger-Teton National Forest.

The plan is designed to protect private property and to allow natural fires to burn in the nearby Palisades Wilderness Study Area.

The Forest Service has pledged to put a buffer around the home ranges of great grays and other owl species, Bedrosian said. As a result his team of biologists has been going "gangbusters" trying to find nest sites.

At 6 a.m. four days later, the biologists were back wandering the woods near Red Top Meadows.

Bedrosian hooted.

"My call must not be that bad — it screwing up both the girls," he said.

On the second take, the biologists opted to switch capture techniques.

A gerbil enclosed in a mesh cage lined with looped monofilament fishing line took the place of the tethered mouse. It's name was Peppermint.

Just shy of two hours into the search the group once again found the mother great gray.

Shortly thereafter, they caught her.

"Got it," Bedrosian shouted.

"Thankfully I didn't have to tackle her this time," he said. "Last time I had to do a flying leap as it got off the trap."

It was routine work for the Beringia South team, but they all seemed energized.



"Peppermint worked," Gura said.

The great gray, whose beady yellow eyes were covered with a ball cap, was a healthy two-pound female.

The bird looked much larger, but that's because she was all fluff.

"There's just so many feathers," Bedrosian said. "They appear larger in size than a great horned owl, but a great horned owl is quite a bit bigger actually."

The plumage is for a reason.

Great grays are a boreal forest species and don't venture much farther south than Jackson Hole in the Northern Rockies. Warming climates figure to shift their ranges north and uphill, Bedrosian said.

"They are an extremely heat-intolerant species," he said.

After measurements and blood samples were taken, the captive owl was fixed with two ID bands. Somewhere in the process a razor-sharp talon punctured the webbing between two of Bedrosian's fingers, and blood trickled.

The team then began to fit the great gray with the GPS backpack.

The transmitter weighs just 30 grams, equivalent to less than 3 percent of her weight.

"We're right at the edge of what technology can do for owls," Bedrosian said.

After she was released, the great gray, now No. A8, settled onto a perch 30 feet up and 100 or so feet away.

She started picking at the foreign straps that secured the transmitter, pausing mostly to peer down at the biologists.

Little does she know that the data the team will glean from her annoying new outfit will help save her soon-to-be mapped home range.

The area around her nest site, Bedrosian said, had been slated for treatment under the Bridger-Teton's wildfire plan.



Research Article

Hiding Without Cover? Defining Elk Security in a Beetle-Killed Forest

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ABSTRACT Recent mountain pine beetle (*Dendroctonus ponderosae*, pine beetle) outbreaks in the western United States have affected nearly 18 million ha of pine (*Pinus* spp.) forest and are unprecedented in spatial extent, severity, and duration, yet little is known about wildlife responses to large-scale insect outbreaks. Elk (*Cervus canadensis*) are important wildlife whose dominant management paradigm on public lands has focused on providing security habitat to increase survival during hunting seasons and to maintain elk presence on public lands to promote hunter opportunity. To assess the effect of pine beetles and associated changes in forest structure on elk security, we used a time series to characterize canopy cover pre- and post-pine beetle outbreak, characterized relative canopy cover among the dominant forest types in the study area post-pine beetle outbreak, and used global positioning system location data from male and female elk to define habitat relationships and security during the archery and rifle hunting seasons. Our study area was within the Elkhorn Mountains of southwest Montana, USA, 2015–2017, which experienced 80% mortality of lodgepole pine (*Pinus contorta*) forests during a pine beetle outbreak that peaked in 2008. We observed an 8.5% reduction in canopy cover within pine beetle-infested lodgepole pine forests, yet canopy cover remained relatively high among other forest types post-outbreak. The top-ranked habitat security models contained positive relationships with canopy cover, distance to motorized routes, terrain ruggedness, and slope with few notable differences among sexes and seasons. Across sexes and seasons, 75% and 50% of elk use was within areas with average canopy cover values $\geq 31 \pm 6.65$ (SD)% and $\geq 53 \pm 5.7\%$ that were an average of $\geq 2,072 \pm 187.93$ m and $\geq 3,496 \pm 157.32$ m from a motorized route, respectively. Therefore, we recommend fall elk security be defined as areas that meet these criteria for minimum canopy cover and distance from motorized routes in the Elkhorn Mountains and in other landscapes with similar forest characteristics and hunting pressures. Although we observed expected reductions in canopy cover within pine beetle-infested forests, defoliation alone did not appear to negatively affect elk security or reduce canopy cover below our management recommendations. Nonetheless, because of the prevalence of standing dead trees in our study area, we recommend future work that investigates the relationships with pine beetle-infested areas post-blowdown because changes in ground structure and costs of locomotion may affect elk habitat and security. © 2019 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

1.3 mi
2 mi

KEY WORDS *Cervus canadensis*, *Dendroctonus ponderosae*, elk, habitat, mountain pine beetle, resource selection function, security.

Recent mountain pine beetle (*Dendroctonus ponderosae*, pine beetle) outbreaks in the western United States have affected nearly 18 million ha of pine forest and are unprecedented in spatial extent, severity, and duration (Chan-McLeod 2006, Meddens et al. 2012, Ivan et al. 2018). Damage caused by pine beetles results in widespread tree mortality, defoliation, and eventual blowdown of dead trees, and can strongly influence

forest community composition and structure, timber production, wildfire dynamics, and wildlife habitat (Jenkins et al. 2008, Klenner and Arsenault 2009, Pfeifer et al. 2011, Simard et al. 2011, Saab et al. 2014). Wildlife responses to pine beetle outbreaks are dynamic and complex, and vary by taxa, sex, season, and the outbreak successional stage (Saab et al. 2014, Ivan et al. 2018). Understanding the effect of pine beetle outbreaks is critical to land and wildlife managers tasked with promoting and conserving wildlife populations where widespread tree mortality has altered wildlife-habitat relationships through changes to forest structure, vegetation communities, and nutrient flow (Chan-McLeod 2006). Although such changes can have profound effects on wildlife and are well

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studied when associated with other natural or managed disturbances (e.g., wildfire, prescribed fire, and timber management), little is known about wildlife responses to large-scale insect outbreaks (Martin et al. 2006, Saab et al. 2014).

Elk (*Cervus canadensis*) have a broad distribution across western North America and can influence vegetation and plant communities (Frank and Evans 1997, Hobbs 2003) and provide economic benefits to regional communities through tourism and hunting (Duffield and Holliman 1988). Elk management on public lands has traditionally focused on providing adequate cover and forage while minimizing motorized routes as the dominate attributes of habitat quality (Hillis et al. 1991, Lyon and Canfield 1991). The management goals under this paradigm are to provide security areas to increase elk survival during the hunting seasons and to maintain elk presence on public lands to promote hunter opportunity (Hillis et al. 1991). However, the traditional management paradigm has been complicated by changes in land use practices and the increase in non-traditional private landowners that are more interested in natural amenities than livestock production and may have restricted public hunting opportunities on parcels that are privately owned (Haggerty and Travis 2006). This results in non-hunted parcels that function as security areas but do not follow the traditional management paradigm on public land and challenge management strategies in areas that strive to maintain or reduce elk population sizes through regulated harvest of adult females (Proffitt et al. 2010, 2013).

Providing additional security areas on public lands through policy changes (i.e., road closures) or habitat improvement projects, has been highlighted as an important management objective to retain elk on public lands and reduce the redistribution of elk to private lands with reduced or eliminated hunting opportunity (Proffitt et al. 2013, Ranglack et al. 2017, DeVoe et al. 2019). Although management paradigms have shifted to accommodate changes in land use practices and attitudes towards elk on private lands, managing for security areas on public lands has remained an important management objective (Ranglack et al. 2017). However, the availability of elk security areas with ample canopy cover may be at odds with the increasing prevalence of pine beetle-killed forests across western North America. The loss of canopy cover is one of the first structural changes in forests after a pine beetle infestation and is arguably the biggest change affecting wildlife (Chan-McLeod 2006). Although specific management recommendations for security habitat have been set for patch size and distance to roads (Hillis et al. 1991), management recommendations for canopy cover have been more varied across the western United States, often relying on general descriptive measures (i.e., heavy cover; Christensen et al. 1993). Although recent work has provided quantitative recommendations for canopy cover based on a meta-analysis across southwest Montana, USA (Ranglack et al. 2017), the work did not include analyses of forest systems affected by pine beetles. The loss of cover after a pine beetle infestation may increase elk vulnerability and require updates to forest management guidelines regarding traditional security

measures on public lands to maintain desired levels of survival and retain elk on public lands during the hunting seasons. Within the context of unprecedented pine beetle outbreaks throughout western North America forests, understanding how insect outbreaks and other disturbances that reduce canopy cover with respect to wildlife security is an important management objective.

We used a multipronged observational approach to characterize the reductions in canopy cover associated with pine beetle outbreaks and the effect on elk security in the Elkhorn Mountains of southwest Montana. We expected to observe a decline in canopy cover in infested areas pre- and post-pine beetle outbreak and a general reduction in canopy cover in infested forests relative to uninfested forests. With respect to elk security, given the anticipated loss of canopy cover associated with the pine beetle outbreak, we expected elk to use security areas characterized by large roadless areas (i.e., security patches) and rugged terrain, and we expected to observe an increase in selection for covariates associated with the traditional security paradigm for both sexes across the gradient of relative risk associated with the archery and rifle hunting seasons (Ranglack et al. 2017, DeVoe et al. 2019).

STUDY AREA

Our study area was broadly defined by the Elkhorn Mountains (2,600 km²; 1,141–2,866 m elevation), a relatively isolated mountain chain in southwest Montana (Fig. 1). The climate was characterized by short, cool summers (17.4°C mean Jul temperature) and long, cold winters (−4.8°C mean Jan temperature) with mean annual precipitation ranging from 263 mm to 959 mm (PRISM Climate Group 2016). The core of the study area consisted of public lands (46%) predominantly managed by United States Forest Service (USFS) and Bureau of Land Management, which were surrounded by low elevation private lands (54%). We conducted our study between 2015 and 2017, 7–10 years after the peak of the pine beetle infestation in 2008. In total, the pine beetle outbreak killed approximately 190 km² (80%) of lodgepole pine forests in the study area.

Lower elevations were dominated by a mixture of open sage-grassland (e.g., big sagebrush [*Artemisia tridentata*], bluebunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*], rough fescue [*Festuca scabrella*], bluegrasses [*Poa* spp.]) and patches of timber (primarily Rocky Mountain juniper [*Juniperus scopulorum*] or Douglas fir [*Pseudotsuga menziesii*]). Additionally, cultivated crops (pasture grasses and leguminous forbs) bordered the northern and southwestern portions of the study area. Upper elevations were dominated by dry coniferous forests (e.g., lodgepole pine, Douglas fir, ponderosa pine [*Pinus ponderosa*]) with small interspersed meadows (USFS et al. 1993). Sympatric ungulates included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and a small population of bighorn sheep (*Ovis canadensis*). Carnivores included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and American black bear (*Ursus americanus*). Grey wolves (*C. lupus*) were transient in the study area.

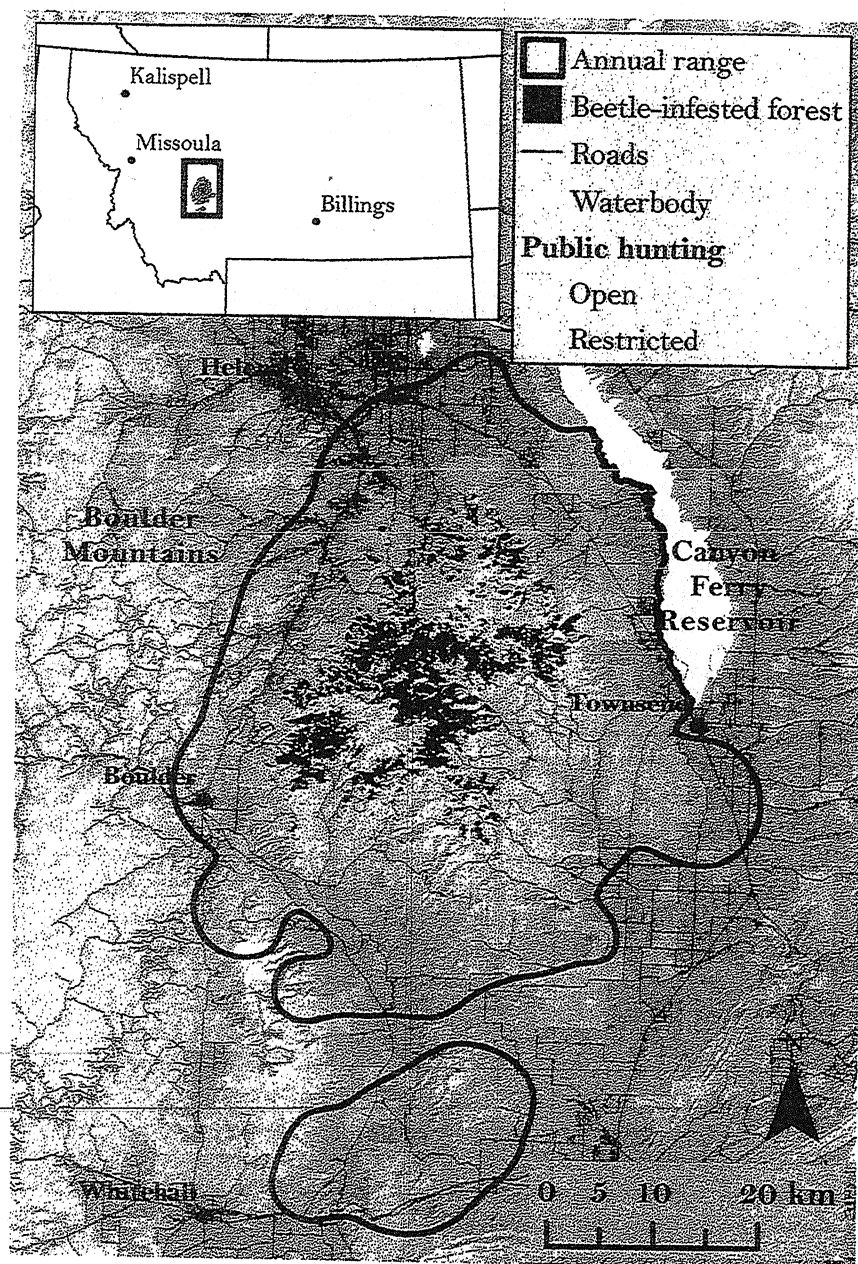


Figure 1. Elkhorn Mountain study area defined by the population-level elk annual range of collared individuals, southwest Montana, USA, 2015–2017. Dark shading in the core of the study area depicts the forests infested by mountain pine beetles. Blue shading depicts lands open to public hunting.

The Elkhorn Mountains are within Montana Fish, Wildlife and Parks hunting district (HD) 380, one of Montana's most popular hunting areas since the early 1960s (DeSimone and Vore 1992, Montana Fish Wildlife and Parks 2018). Estimated hunter effort has continued to increase since the 1960s with record highs of 3,936 hunters and 31,786 hunter days in 2015. Male elk hunting in this region is particularly popular because of a unique spike regulation that generates a relatively high male:female ratio and a mature male age structure. When this study occurred (2015–2017), anyone with a general hunting license could harvest a spike or antlerless elk during the archery season. During the rifle season anyone with a general hunting license could harvest a spike, and youth

hunters could harvest an antlerless elk. For each year of the study, the number of limited either-sex permits was 120. The number of limited B licenses (antlerless elk) valid for either the entire hunting district or a portion of the hunting district was 700 in 2015, 800 in 2016, and 800 in 2017.

METHODS

Canopy Cover Characterizations

We used aircraft survey data collected by the United States Department of Agriculture Forest Health Protection Aviation Program to delineate pine beetle-affected areas as observed by tree canopy discoloration indicating mortality

(USFS 2017, 2018). However, the pine beetle delineations generated from aerial flights did not strictly mirror the patchy mosaic on the landscape and occasionally included grassland meadows or other landcover classifications not affected by pine beetles. To reduce the contamination of non-beetle-killed areas, we clipped the polygons delineating pine beetle infestations to include only the areas that overlapped with lodgepole pine or lodgepole pine shade-intolerant mixed forest classifications as defined by the Vegetation Mapping Program (VMap; USFS 2014).

We characterized canopy cover in pine beetle-infested forests using a time series from the Rangeland Analysis Platform (RAP; Jones et al. 2018) spanning 1990–2017, inclusive of the pine beetle outbreak in the Elkhorn Mountains. The RAP uses a combination of remotely sensed and ground-based data to predict per-pixel (30 m × 30 m) percent canopy cover across the western United States. Although developed for rangelands, the RAP model is an effective tool for describing changes in canopy cover through time with a fine-scale (annual) time series not available in other canopy cover layers (i.e., LANDFIRE, National Land Cover Database). To assess changes in canopy cover within pine beetle-infested forests over time, we characterized the percent change from historical canopy cover levels prior to the pine beetle outbreak (1990–2000) within the 3 largest pine beetle polygons in the study area, which totaled 111 km² and accounted for nearly 60% of the lodgepole pine forests infested by pine beetle.

To assess changes in canopy cover between pine beetle-infested forests and uninfested forests, we summarized the percent canopy cover in infested and uninfested lodgepole pine forests and ponderosa pine and Douglas fir forest classifications. In aggregate, these forest types contained 99% of the forested landscape within the study area. We characterized the mean (±SD) percent canopy cover in each forest type using VMap canopy cover estimates from 2013 (USFS 2014). These estimates represented a mean response of canopy cover defoliation associated with pine beetle outbreaks approximately 5 years after peak infestation and were the most recent estimates for the Elkhorn Mountains after the pine beetle infestation. Moreover, the VMap methods used to estimate canopy cover were specifically developed to note changes in canopy cover associated with pine beetle outbreaks (S. R. Brown, USFS, personal communication).

Security Habitat Modeling

During the winters of 2015 and 2017, we captured adult (>1.5 yr) elk by helicopter net-gunning and darting in accordance with an approved animal welfare protocol (Institutional Animal Care and Use Committee Project Number: FWP09-2014, FWP10-2017). We deployed remote-upload collars (Lotek Wireless model LifeCycle, New Market, Ontario, Canada) programmed to transmit 1 location every 23 hours through the Globalstar satellite network, the exact timing of which varied across collars. Average fix success excluding data transmission gaps was 96 ± 3%, indicating negligible landcover-induced fix bias

(Johnson and Gillingham 2008). Collars on adult females remained on the animal for life and on adult males were programmed to automatically release after 4 years. We censored all locations with positional dilution of precision >10 to reduce spatial imprecision (D'eon and Delparte 2005).

Our primary objective was to characterize elk selection to define elk security habitat and inform land management practices on public lands. We focused our security habitat modeling on individuals that remained on lands open to public hunting and retained in our dataset only individuals that had >50% of their GPS locations on lands open to public hunting (i.e., public lands or private lands enrolled in Montana Fish, Wildlife, and Parks hunter access program). To further target the periods when hunting pressure most strongly influenced elk behavior, we restricted our analyses to legal hunting hours defined as 0.5 hours before and after sunset.

We developed separate sex-season resource selection functions using a used-available design (Manly et al. 2002) and generalized linear mixed-effect models with a random intercept for each individual to account for autocorrelation within an individual and unequal sample sizes among individuals (Gillies et al. 2006). We fit mixed-effect models using the lme4 R package (Bates et al. 2015) and the inverse link function. Our used dataset was defined by the locations collected from GPS collars, whereas we sampled availability at a 1:15 used to available ratio within each individual's annual 100% minimum convex polygon. The 1:15 ratio ensured a sufficient sample to avoid numerical integration error and convergence issues given the single location per day fix rates of the deployed GPS collars (Northrup et al. 2013). We characterized resource selection separately for the archery and rifle hunting seasons, which reflected varying degrees of perceived risk from low to high. Following the legal definitions, the archery season was the 6-week period starting on the first Saturday in September, and the 5-week rifle season started 5 weeks prior to the Saturday after Thanksgiving.

We evaluated multiple landscape attributes associated with elk vulnerability including 3 definitions of security patches, percent canopy cover, and distance to motorized routes (Table 1). Although commonly used in elk security models, we did not include a covariate that described public or private land ownership because our analyses were restricted to individual elk that predominantly used lands that allowed public hunting. We derived our criteria for defining security patches from Hillis et al. (1991), which has been widely incorporated into USFS security habitat management standards, and defined security patches as contiguous areas of ≥100 ha located ≥0.8 km from an open motorized route. To evaluate the importance of canopy cover in definitions of elk security, the 2 additional security patch covariates included contiguous areas that contained ≥50% coverage of ≥15% and ≥30% canopy cover. In addition to the covariates associated with the traditional management paradigm, we evaluated the importance of terrain covariates associated with security: slope and ruggedness. For ruggedness we used the vector ruggedness measure (VRM), a unitless measure of landscape ruggedness integrating variation in slope and

Table 1. Covariates used in male and female elk security habitat modeling, Elkhorn Mountains, southwest Montana, USA, 2015–2017.

Covariate	Description	Functional forms ^a	Reference
Security patch	Contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route.	Binary	Hillis et al. (1991), Christenses et al. (1993), DeVoe et al. (2019)
Security patch with canopy cover	Contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route and with at least half of the security patch containing 15% and 30% canopy cover as 2 different covariates.	Binary	Hillis et al. (1991), Christenses et al. (1993), DeVoe et al. (2019)
Canopy cover	Percent canopy cover.	Ps	USFS 2014, Ranglack et al. (2017), DeVoe et al. (2019)
Distance to motorized route	Distance (m) to motorized 2-track, dirt, or paved road designated as open to public use within each respective hunting season.	Ps	McCorquodale et al. (2003), Ranglack et al. (2017)
Ruggedness	Vector ruggedness measure (VRM): a unitless measure of landscape ruggedness integrating variation in slope and aspect.	Ps	Hillis et al. (1991), Sappington et al. (2007), DeVoe et al. (2015), Lamont et al. (2019)
Slope	Slope in degrees.	Sq	Hillis et al. (1991), Ranglack et al. (2017), DeVoe et al. (2019)

^a Ps = pseudothreshold, Sq = squared or quadratic, binary signifies categorical covariate for which we did not consider functional forms.

aspect (Sappington et al. 2007). Following a large body of literature from regional studies modeling seasonal habitats and security areas for elk and other ungulates, we used a pseudothreshold (natural log) functional form for canopy cover, distance to motorized routes, and ruggedness, and a quadratic functional form for slope (Sawyer et al. 2007; Proffitt et al. 2010, 2013; Ranglack et al. 2017; DeVoe et al. 2019).

We used a tiered approach to progress from univariate to multivariate models evaluating the traditional security metrics and landscape attributes. In each tier, we identified the top-ranked model for each sex and season using corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). In the first tier we fit univariate models for each of the security patch covariates (with and without canopy cover) to evaluate the importance of canopy cover in defining security patches. In the second tier we fit 5 candidate models containing multiple combinations of covariates associated with the traditional management paradigm on public lands. Lastly, in the third tier, we added slope and terrain ruggedness as a paired combination to evaluate the addition of landscape covariates. With the final model we generated predictive plots for each continuous covariate while holding all other covariates at their mean value. To provide management recommendations for covariates with a pseudothreshold form, we calculated cumulative elk use as the cumulative area under the curve starting with the largest probability value to target the covariate range with the highest relative probability of use for each sex and season. We then identified the range of covariate values that corresponded to 75% and 50% of the area under the curve and used the minimum values within the range to define thresholds for security and preferred security areas, respectively. These values served as the basis for our management recommendations and reflect the narrowest covariate range associated with 75% (security) and 50% (preferred security) of elk use. To minimize the influence of extreme

outliers on the area under the curve and corresponding management thresholds, we removed from the available dataset covariate values that were well beyond the distribution of values observed in the used dataset. For quadratic covariates (i.e., slope), we noted the covariate value that maximized the relative probability of use for each sex and season.

We preformed model validation using a k-fold cross-validation within an iterative process where we withheld the locations for each 5 folds, fit an exponential resource selection function (RSF) with the data that were retained, and then predicted the fitted values for the observations that were withheld (Boyce et al. 2002). We then summed the occurrence of used locations within 10 equal-area RSF bins and evaluated the correlation between the frequency of occurrence and the relative RSF score using the Spearman's rank correlation (Boyce et al. 2002). The adjusted frequencies should be highly correlated with the relative RSF if the model performs well (Boyce et al. 2002). We conducted all analyses and data processing in the R environment for statistical computing (R Core Team 2018) in combination with the sf (Pebesma 2018) and raster (Hijmans 2017) packages for spatial analysis and the tidyverse suite (Wickham 2017) for data manipulation and visualization.

RESULTS

Canopy Cover

The reductions in percent canopy cover below historical levels before the pine beetle outbreak (1990–2000) mirrored the pine beetle outbreak timeline with a 2–3-year lag after the initial infestation (Fig. 2). Between the peak pine beetle outbreak in 2008 and the following 2 years, there was an average $8.5 \pm 2.5\%$ reduction in canopy cover within the pine beetle-infested areas we evaluated. After the pine beetle outbreak and associated canopy cover declines, canopy cover began to increase in 2010 and 2011, nearly approaching historical averages by 2015, 7 years after peak infestation.

Best CC = LFP

7 yr

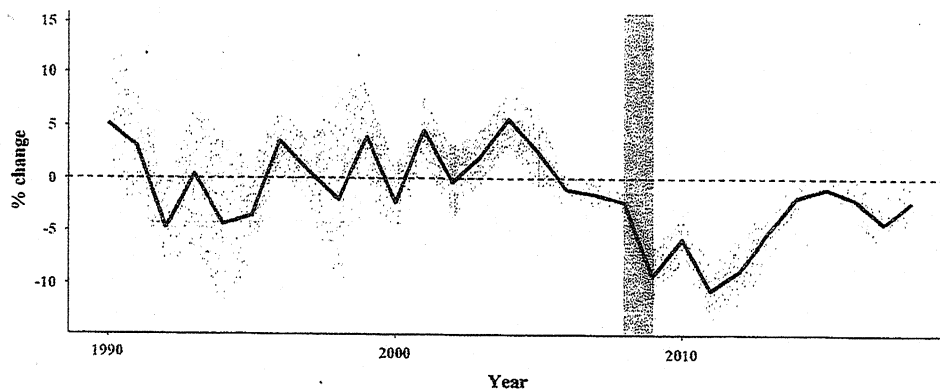


Figure 2. Twenty-seven-year (1990–2017) time series of the mean ($\pm$ SD) percent change in canopy cover from the historical average (1990–2000) for the 3 largest patches of forest infested by mountain pine beetles within the Elkhorn Mountain study area, southwest Montana, USA, 2015–2017. The year of peak beetle infestation (2008) is shaded.

Within forested portions of the study area, forests classified as uninfested lodgepole pine had the highest values for canopy cover post-pine beetle infestation with a mean of $77 \pm 14.6\%$ (Fig. 3). Similar to the trends described in the canopy cover time series, there was an 8% reduction in canopy cover in infested lodgepole forests ($\bar{x} = 69 \pm 15\%$). Canopy cover in pine beetle-infested lodgepole forests remained higher than canopy cover in uninfested Douglas fir and ponderosa pine forests (including both infested and uninfested stands), which had $54 \pm 18.9\%$ and $27 \pm 8.7\%$ canopy cover, respectively.

Security Habitat Modeling

We captured 59 adult (male = 24, female = 35, total excludes 3 individuals that died during capture) elk during the winters of 2015 and 2017. To evaluate security on lands open to public hunting, we censored 4 males and 12 females that had $>50\%$ of their GPS locations on private lands that restricted hunting during the archery and rifle seasons. Among censored elk, a mean of $74 \pm 15\%$ of male and female GPS locations were in areas with restricted hunting access. Lastly, we censored 3 individuals (males = 2, females = 1) without any daytime locations within a hunting

season. Among the remaining 40 (male = 18, female = 22) individuals, there were 72 animal-years with an average of 30 ± 20.5 GPS locations for each individual-season and an average of 572 ± 235 GPS locations for each sex-season grouping.

In the first tier of model selection, where we evaluated the addition of 15% and 30% as canopy cover thresholds to define security patches, security patches defined without a canopy cover threshold were top-ranked for males in both seasons and for females during the archery season (Table 2). The exception was females during the rifle season where security patches with 30% canopy cover were top-ranked. Nonetheless, there was a large degree of uncertainty in the top-ranked model and a difference of only 0.68 AIC_c units among the 3 univariate models. Because there was not a clear top-ranked model for females during the rifle season, and to have continuity among the second tier sex-season models with respect to security patch definitions, we selected security patches defined without canopy cover as the top model for all sex-seasons (Table 2).

In the second tier we evaluated 5 univariate and multivariate combinations of the traditional security metrics (i.e., distance to motorized routes, canopy cover, and security

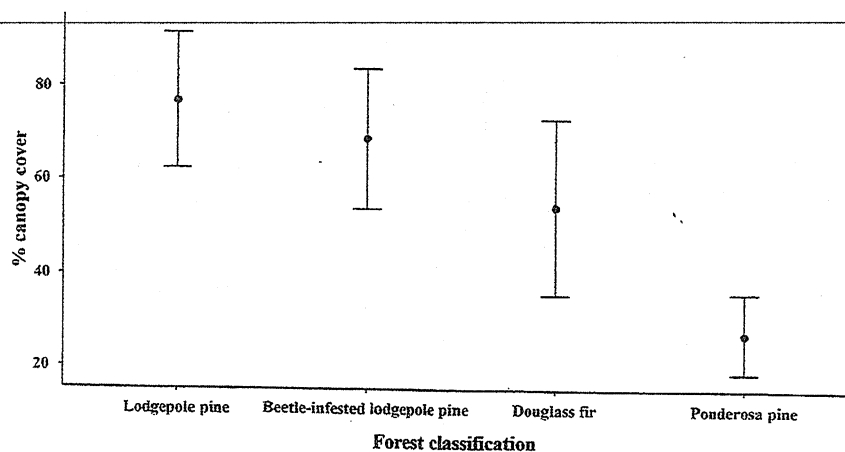


Figure 3. Average canopy cover percentages ($\pm$ SD) within uninfested and pine beetle-infested lodgepole pine, Douglas fir, and ponderosa pine forest classifications, Elkhorn Mountains, southwest Montana, USA, 2015–2017.

Table 2. Habitat security model selection results for tiers 1–3 comparing used and available locations for male and female elk in the archery and rifle hunting seasons, Elkhorn Mountains, southwest Montana, USA, 2015–2017. Models are arranged by corrected Akaike's Information Criterion (AIC_c) ranking. We also present the number of parameters (K) and model weight (w_i).

Model tier	Sex-season	Model ^a	K	AIC _c	ΔAIC _c	w_i
Tier 1: Security patch	Female-archery	Security.00	3	6,399.02	0.00	0.67
		Security.30	3	6,401.72	2.70	0.17
		Security.15	3	6,401.86	2.85	0.16
	Female-rifle	Security.30	3	4,570.29	0.00	0.41
		Security.00	3	4,570.86	0.56	0.31
		Security.15	3	4,570.97	0.68	0.29
	Male-archery	Security.00	3	3,916.05	0.00	1.00
		Security.15	3	3,984.58	68.53	0.00
		Security.30	3	3,984.68	68.62	0.00
	Male-rifle	Security.00	3	2,132.94	0.00	0.96
		Security.30	3	2,140.85	7.91	0.02
		Security.15	3	2,140.85	7.91	0.02
Tier 2: Traditional security	Female-archery	Canopy cover + DMOT	4	6,267.63	0.00	1.00
		Canopy cover	3	6,293.88	26.25	0.00
		Canopy cover + security.00	4	6,294.21	26.59	0.00
		DMOT	3	6,366.89	99.26	0.00
		Security.00	3	6,399.02	131.39	0.00
		Canopy cover + DMOT	4	4,328.85	0.00	1.00
	Female-rifle	Canopy cover + security.00	4	4,363.95	35.10	0.00
		Canopy cover	3	4,382.79	53.94	0.00
		DMOT	3	4,527.33	198.49	0.00
		Security.00	3	4,570.86	242.01	0.00
		Canopy cover + DMOT	4	3,902.77	0.00	0.78
		DMOT	3	3,905.31	2.55	0.22
	Male-archery	Canopy cover + security.00	4	3,913.24	10.47	0.00
		Security.00	3	3,916.05	13.29	0.00
		Canopy cover	3	3,974.72	71.95	0.00
		Canopy cover + DMOT	4	2,096.46	0.00	0.99
		Canopy cover + security.00	4	2,105.41	8.96	0.01
		Canopy cover	3	2,110.71	14.25	0.00
	Male-rifle	DMOT	3	2,121.66	25.20	0.00
		Security.00	3	2,132.94	36.48	0.00
		Canopy cover + DMOT + Slope ² + ruggedness	7	6,233.22	0.00	1.00
		Canopy cover + DMOT	4	6,267.63	34.41	0.00
		Canopy cover + DMOT + slope ² + ruggedness	7	4,305.30	0.00	1.00
		Canopy cover + DMOT	4	4,328.85	23.54	0.00
Tier 3: Traditional and landscape security	Female-archery	Canopy cover + DMOT + slope ² + ruggedness	7	3,808.99	0.00	1.00
		Canopy cover + DMOT	4	3,902.77	93.77	0.00
	Female-rifle	Canopy cover + DMOT + slope ² + ruggedness	7	2,029.19	0.00	1.00
		Canopy cover + DMOT	4	2,096.46	67.27	0.00
	Male-archery	Canopy cover + DMOT + slope ² + ruggedness	7			
		Canopy cover + DMOT	4			

^a Security.00 = security patch with no canopy cover requirement; security.15 and security.30 = security patch with ≥50% coverage of 15% and 30% canopy cover; DMOT = distance to motorized route.

patches defined without a canopy cover threshold from the first tier). In all sex-seasons the multivariate model containing distance to motorized routes and canopy cover was top-ranked by a minimum of 2.55 ($\bar{x} = 18.21 \pm 15.06$) AIC_c units (Table 2). In general, there was relatively more support for multivariate models than for univariate models and the least support for security patches as a single predictor of elk security.

In the third tier, the inclusion of slope and ruggedness improved AIC_c ranking in all sex-seasons by a minimum reduction of 23.5 ($\bar{x} = 57.74 \pm 31.97$) AIC_c units (Table 2), resulting in the same model structure in the final model for all sex-seasons, which contained canopy cover, distance to motorized routes, ruggedness, and slope covariates (Appendix A). Across all sex and season combinations, the Pearson's correlation coefficients were ≤0.4.

The top-ranked habitat security models performed well with a strong correlation between area-adjusted frequencies and the

relative RSF for all sexes and seasons (female-archery: $r_s = 0.93$, $P < 0.001$, female-rifle: $r_s = 0.99$, $P < 0.001$, male-archery: $r_s = 0.97$, $P < 0.001$, male-rifle: $r_s = 0.91$, $P < 0.001$). Additionally, with only a few exceptions the top-ranked models produced similar results across sexes and seasons (Fig. 4). There was a positive pseudothreshold relationship with canopy cover, indicating increased selection for areas that had relatively more canopy cover, and the relationship was stronger for females than for males. Males during the archery season had the weakest relationship with canopy cover and a coefficient estimate that was nearly zero (Appendix A), resulting in a flat prediction line across the observed values of canopy cover (Fig. 4). Although between-season differences in selection for canopy cover were modest, both sexes selected for higher canopy cover values in the rifle season than in the archery season. The stronger relationship for females resulted in higher canopy cover thresholds associated with security and preferred security areas in both seasons. Females during the

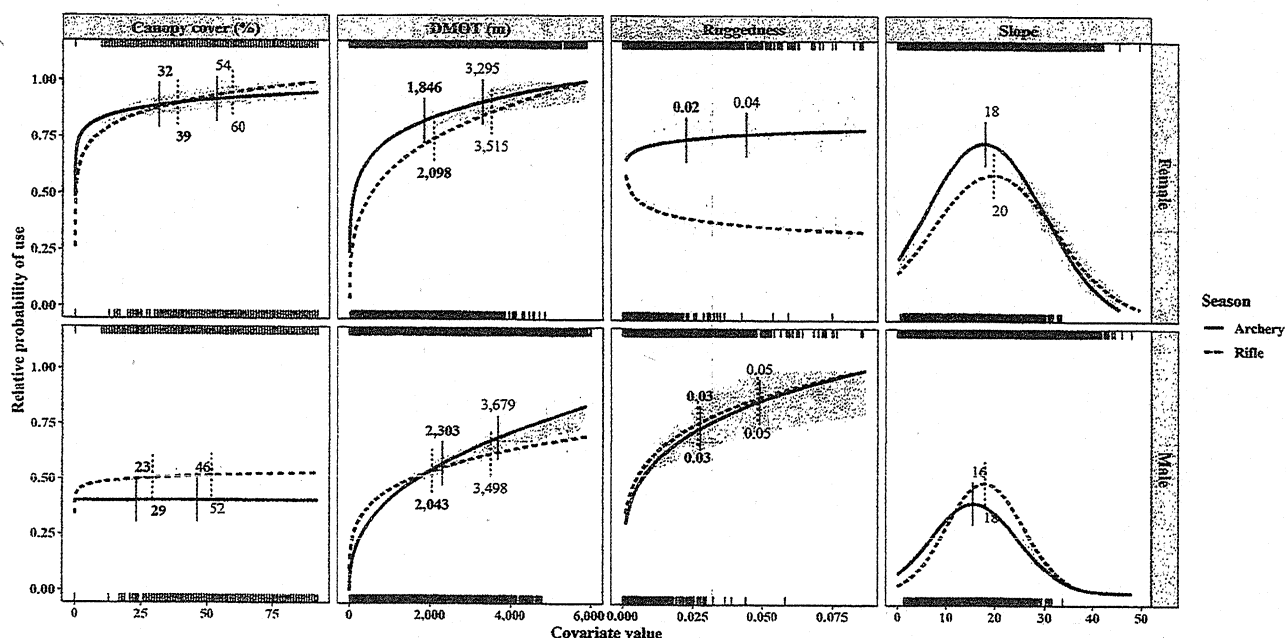


Figure 4. Prediction plots showing the relationship with the relative probability of use ($\pm 95\%$ CI) for each covariate (columns), sex (rows), and season (archery = solid line, rifle = dashed line) with all others held at their mean value, for elk in the Elkhorn Mountains, southwest Montana, USA, 2015–2017. The upper rug represents the available locations, whereas the lower rug represents the used locations. Threshold values for the archery (solid vertical lines) and rifle (dashed vertical lines) seasons represent the minimum covariate values for security and preferred security areas as defined by the 75% and 50% cumulative elk use thresholds, respectively. DMOT = distance to motorized route.

rifle season selected security areas containing canopy cover values $\geq 39\%$ and preferred security areas containing canopy cover values $\geq 60\%$.

The relationship with distance to motorized routes was positive in all top-ranked season-sex models, indicating increasing selection for areas farther from roads. This relationship was steeper for females than for males and similar across the rifle and archery hunting seasons (Fig. 4). There was strong overlap in covariate values delineating security and preferred security among both sexes and seasons. The most conservative values were for males during the archery season where security areas were defined as being $\geq 2,303$ m from a road and preferred security areas were $\geq 3,679$ m from a road.

The ruggedness covariate had the most varied results among sexes and seasons. Females had a positive association with ruggedness during the archery season and a negative relationship during the rifle season (Fig. 4). In contrast, the relationship was positive for males with little difference between the rifle and archery season, both of which had a stronger relationship relative to females. The stronger relationship for males resulted in relatively high ruggedness thresholds associated with security and preferred security areas, which occurred in areas with ruggedness values ≥ 0.03 and ≥ 0.05 , respectively. Lastly, the quadratic functional form for slope indicated an average optimal slope value of $18 \pm 1.6^\circ$ with little variation among sexes or seasons (Fig. 4).

DISCUSSION

Our study combined canopy cover characterizations with wildlife habitat modeling after a pine beetle infestation to assess the effect of pine beetle on elk security through

reductions in canopy cover. We observed an 8.5% reduction in canopy cover within pine beetle-infested lodgepole pine forests compared to historical levels before the pine beetle outbreak. Nonetheless, canopy cover in pine beetle-infested forests remained relatively high ($\bar{x} = 69 \pm 15\%$) and had higher cover values than uninfested Douglas fir and ponderosa pine forests by 15% and 42%, respectively. The presence of canopy cover was an important component in defining elk security and was an important predictor of male and female elk distributions in the archery and rifle hunting seasons. However, given the relatively high degree of cover offered by lodgepole pine forests, including those affected by pine beetles, the changes in cover associated with defoliation after the pine beetle infestation were relatively minor and did not result in a meaningful reduction in canopy cover below the thresholds used to define security and preferred security areas. Across sexes and hunting seasons, elk security areas contained average canopy cover values $\geq 30 \pm 6.7\%$ and contained 75% of elk use on the landscape. Preferred security areas, which contained 50% of elk use on the landscape contained canopy cover values $\geq 53 \pm 5.7\%$. In general, although we observed expected reductions in canopy cover within pine beetle-infested forests, the level of reductions that we observed in our study did not appear to negatively affect elk security after the pine beetle infestation.

In addition to the selection for areas with higher canopy cover, security habitat in the Elkhorn Mountains was characterized by positive associations with increasing distances from motorized routes, relatively rugged slopes, and moderate slope angles of 18° . In general, these findings corroborate with other studies characterizing elk security

9025: 1.7 mi

and habitat (Lyon and Canfield 1991, McCorquodale et al. 2003, Ranglack et al. 2017, DeVoe et al. 2019). Although the traditional definition of an elk security patch that has been broadly incorporated into forest management (i.e., contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route; Hillis et al. 1991) did not receive strong support among our candidate model set, our work lends credence to the importance of canopy cover and distance to motorized routes in defining elk security.

The importance of canopy cover in defining and managing elk security on public lands is varied across the western United States. In areas with expansive forest cover, elk security can be influenced by road management alone, yet where forest cover is limited or patchy, incorporating canopy cover into definitions of elk security is also important (Christensen et al. 1993, Unsworth et al. 1993). In contrast to the definitions for distances to motorized routes and patch size, which have largely followed the Hillis paradigm (Hillis et al. 1991), the varied importance of canopy cover has resulted in a variety of arbitrary cover definitions used to define elk security (Christensen et al. 1993). A recent meta-analysis incorporating data from 325 female elk in southwest Montana that occupied public lands and private lands with restricted hunter access recommended managing for areas with $\geq 13\%$ canopy cover that are $\geq 2,760$ m from motorized routes when defining elk security (Ranglack et al. 2017). Their recommendations were based on the covariate value that corresponded to half of the change in the relative probability of use over the observed covariate range (Ranglack et al. 2017). Although these methods may be well suited for relationships between use and cover characterized by pseudothreshold curves with a sharp rollover, they are arbitrary in the selection of 0.5 and less appropriate for curves with a broad rollover where half of the total gain across the x - and y -axes may not result in meaningful management recommendations. Rather than provide a single minimum value, our approach provided a range for canopy cover and distance to motorized routes based on the cumulative elk use and our definitions of security and preferred security areas (i.e., 75% and 50% area under the curve, respectively). Our results suggest that minimum canopy cover values between 23% and 60% and distances to motorized routes between 1,846 m and 3,679 m characterize most elk use within our Elkhorn Mountain study area for both sexes in both the archery and rifle hunting seasons. Rather than provide a single minimum recommendation, the range of covariate values and their relationship with elk use provides an alternative approach to providing management recommendations that better accommodates the varied shapes of our predictive curves and meaningfully translates to elk resource use.

2036: 1.4
12030: 2.2

In addition to different methodologies for defining threshold values, there were important differences between the study areas and study designs that may have contributed to the more conservative recommendations regarding canopy cover and security from this study compared to Ranglack et al. (2017) and Hillis et al. (1991). First, Ranglack et al. (2017) included female elk on public and

private lands when defining elk security. In contrast, our recommendations were developed for male and female elk that predominately occupied lands open to unrestricted public hunting and censored elk on private lands with restricted hunter access where elk may be less reliant on areas of dense canopy cover far from motorized routes because hunting pressure is relatively lower. Second, although we were unable to estimate hunter densities specifically for lands open to unrestricted public hunting within our study area or across Montana, the Elkhorn Mountains hunting district (HD 380) is subject to relatively high hunting pressure with record highs of 3,936 hunters and 31,786 hunter days in 2015. Moreover, on average the Elkhorn Mountains received 5.4 times (range = 1.4–35) more hunters and 5.7 times (range = 1.4–28) more hunter days than the populations from Ranglack et al. (2017). Lastly, in contrast to Hillis et al. (1991), which was conducted in densely forested systems in western Montana, our study was located in southwest Montana where cover is patchily distributed. Given our focus on public lands in the most heavily hunted district in Montana with patchily distributed forest cover, one would expect elk to have stronger selection for forest cover and security areas than when pooling elk across areas with restricted and unrestricted hunting access (Ranglack et al. 2017) or when working in systems that are largely forested (Hillis et al. 1991).

Although our results indicated elk continued to use areas affected by pine beetles post-infestation during the hunting season, regionally there have been mixed results regarding elk use of pine beetle-infested forests. In south-central Wyoming, USA, Lamont et al. (2019) reported that during summer female elk avoided pine beetle-infested forests during nearly all parts of the day and selected for intact coniferous forests during daytime. The selection for intact forests during daytime in summer highlights the need for thermal refuge, which may be compromised in pine beetle-infested forests (Lamont et al. 2019). In contrast, Ivan et al. (2018) documented an increase in the use of pine beetle-infested forests by elk, mule deer, and moose during summer months across Colorado, USA, presumably influenced by increases in understory forage associated with the decrease in canopy cover post-defoliation. Given the host of dynamic factors that can influence wildlife response to pine beetle infestations, many of which are spatially and temporally variable and difficult to quantify over broad spatial scales (i.e., number of downed trees), regional and taxonomic generalizations may prove difficult given the limited number of studies examining wildlife responses to pine beetle infestations that have been completed currently (Saab et al. 2014).

thermal refuge

An additional consideration in interpretations and applications of our work was the successional stage of pine beetle-infested forests in our study area. An increase in fallen trees is presumed to influence wildlife mobility in pine beetle-infested forests with a hypothesized reduction in use associated with increased costs in mobility (Saab et al. 2014, Lamont et al. 2019). Our study occurred between 2015 and 2017, 7–10 years after the peak of the pine beetle infestation

in 2008, yet most of the infested trees were standing dead. Given the lack of downed trees during our study period, our results are specific to the period post-defoliation but before tree blowdown. Although Lamont et al. (2019) did document an increase in downed trees in pine beetle-infested forests, their study also occurred when trees were just beginning to fall, 3–7 years following the peak outbreak. Although downfall in infested areas was not widespread, the avoidance of pine beetle-infested areas during all parts of the day in their study area was suggestive of a down-tree effect and lends correlative support to elk avoiding pine beetle-infested areas and the associated increase in locomotion costs (Lamont et al. 2019). In Colorado, Ivan et al. (2018) did not describe the degree of downfall across their broad study region but did see increases in ungulate use of pine beetle-infested forest across 3 different severities (10%, 50%, and 90% mortality) spanning 0–11 years after initial outbreak.

As pine beetle-infested forests transition from standing dead to blowdown, understanding the effect on elk habitat and security is an important consideration. Given the large degree of canopy cover provided by lodgepole forests on public lands and the large percentages that have been affected throughout the western United States, relatively minor avoidance of these areas could result in a notable net loss of habitat that provides demographic benefits through increased security and thermal cover. As pine beetle-infested forests continue to mature with increasing proportions of fallen trees, assessing the degree to which these forests are selected or avoided by elk and the effect on demography will be a management priority. Additionally, the management of adjacent or nearby intact forests may become increasingly important in providing elk security as infested stands mature and potentially become inadequate for providing elk security.

MANAGEMENT IMPLICATIONS

We recommend that managers include measures of canopy cover and distance to motorized routes in definitions of elk security and encourage managers to implement seasonal or permanent road closures in areas with forest canopy cover to provide elk security during hunting seasons. In the Elkhorn Mountains and other landscapes with similar forest characteristics and hunting pressures, we recommend managing for security with canopy cover values of 23–60% and distance from motorized routes of 1,846–3,679 m based on our definitions of security and preferred security areas, respectively. Where possible, the implementation of more stringent objectives at the upper end of the canopy cover and distance to road thresholds will more strongly reflect preferred security areas. In addition, locating security areas in relatively rugged terrain and moderate slope angles (i.e., 18°) can further enhance elk security. Given the relatively small difference in selection patterns between males and females and the archery and rifle hunting seasons, these recommendations are appropriate for both sexes and both the archery and rifle hunting seasons. Managing for these habitat security attributes on public lands may help to

reduce the redistribution of elk to private lands that restrict hunting during the archery and rifle seasons. In the presence of pine beetle infestations, we also recommend prioritizing intact forests with high canopy cover to help retain security areas as infestations mature and blowdown, potentially further affecting habitat conditions within infested forests. Because of the relatively narrow temporal window of our study, approximately 7–10 years after the beetle infestation, we recommend future work that investigates the relationships with pine beetle-infested areas post-blowdown as changes in ground structure may provide the biggest effect to habitat and security for elk and other ungulates.

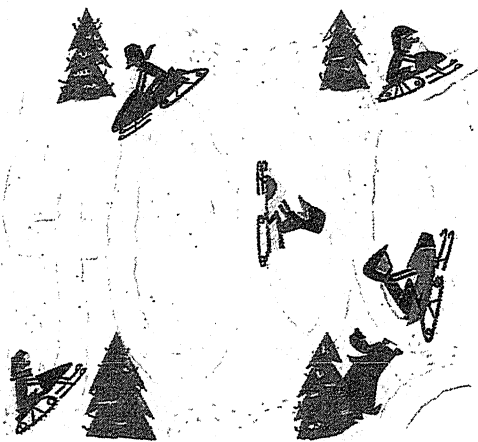
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OUTDOORS REPORT



4,000 Miles of groomed snowmobile trails in Montana.

Waterfowl up, other birds down

The latest report on U.S. bird populations offers a tale of two trends, one hopeful, one dire. Published by 33 leading science and conservation organizations and agencies, the "2022 U.S. State of the Birds Report" is the first comprehensive look at the nation's birds since a landmark 2019 study showed the loss of nearly 3 billion birds in the United States and Canada in 50 years. Key findings from the new report:

- ▶ Waterbirds and ducks in the U.S. have increased by 18 percent and 34 percent, respectively, since 1970.
- ▶ U.S. grassland birds are among the fastest declining, with a 34 percent loss during the same period.
- ▶ Over half of U.S. bird species are declining. The report advises that meeting declining birds' needs will require a strategic combination of partnerships, incentives, science-based solutions, and public will to dramatically scale up the conservation of fast-disappearing bird habitats such as native grasslands.



Peak migration is usually the last week of March. But check the Freezout web page before you go.

WILDLIFE WATCHING

FWP web page updates Freezout waterfowl count

Each year in late winter, photographers and bird watchers thrill to the sight of snow goose "tornadoes" rising up from Freezout Lake, about 20 miles northwest of Great Falls. But the spectacle is witnessed only by those who show up on the right days.

Tens of thousands of migrating ducks, geese, tundra swans, and other birds pass through this area on their way to northern nesting grounds. The lake and surrounding barley fields provide an essential pitstop for resting and refueling during the long journey.

Because the birds stay only a few weeks, visitors need to know what stage the migration is in before making the drive to Freezout Lake

Wildlife Management Area (WMA). On average, the last week of March sees the largest number of migrating waterfowl, but that can change due to storms and other weather.

FWP has a new web page that includes daily Freezout Lake updates during spring and fall migrations. The page also includes information on the WMA's history and management, as well as hunting, wildlife watching, and trapping opportunities and a detailed map.

To view the page, visit fwp.mt.gov and click on the Conservation tab at the top. From the menu on the left, select "WMAs," then search for "Freezout Lake WMA." On the Freezout Lake WMA page, click on the "Freezout Lake WMA Story Map" link under the photo. ■

CLIMATE

State climatologist predicts even warmer days ahead

Dr. Kelsey Jencso, state climatologist with the Montana Climate Office, believes that by 2069, some areas of Montana can expect up to five more weeks of above-90-degree days each year.

During a Zoom conference on climate change this past November, Jencso explained his prediction by pointing out that, over the past 65 years, the state's temperature has increased 0.42 degree per decade while the national average is 0.26 per decade. That's an increase of 2.7 degrees in the past 65 years, which is also above the national average.

The greater rate of change is due to Montana's higher altitude, making it more sensitive to temperature

fluctuations, Jencso told the conference, organized by the Montana League of Women Voters. He also said:

▶ Total precipitation from spring rains has increased by 1.3-2 inches per year in eastern Montana and declined by 0.9 inch in western Montana.

▶ By mid-century, computer models predict a 5-degree temperature increase in eastern and north-central Montana and a 4-degree increase in central and western Montana.

▶ Also by mid-century, eastern Montana is expected to have 39 more days above 90 degrees each year and western Montana will see 10 to 15 additional days of 90-degree-plus temperatures. ■



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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 Partners 'Flight

Montana Bird Conservation Plan
Version 1.0 - Jan. 2000

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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 [Bull and Holthausen recommended > 8 snags/ha, at least 20% of which are > 50 cm, and . 100 logs/ha, with a preference for logs > 38 cm]
- Refrain from sanitation cutting of insect-killed trees within the 20% of lands managed for old-growth; limit firewood cutting to snags less than 40 cm and discourage use of larch, ponderosa pine, and broadleaf species (McClelland et al. 1979).

Prescribed Fire: (see also section on Burned Forests)

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

Timber Harvest:

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

Science

FINDINGS

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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-1990s, 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.

SLEUTHING FOR HABITAT CLUES

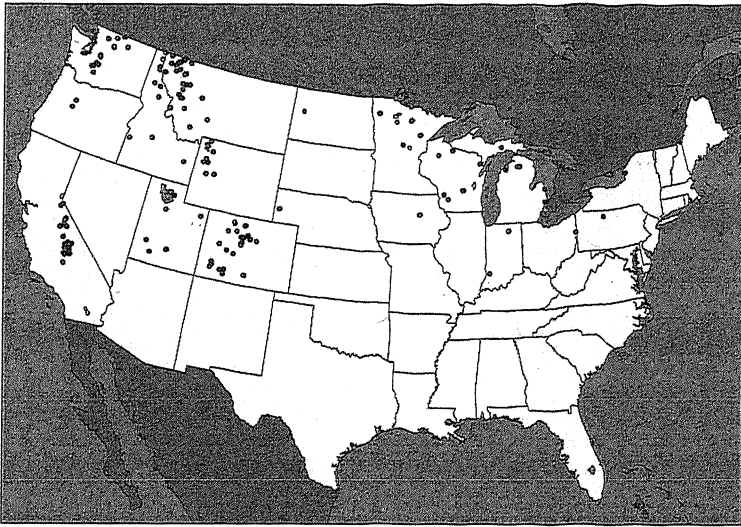
To home in on the environmental features that determine the wolverine's distribution, the team employed three broad-scale habitat maps: one that depicts potential natural vegetation types in the contiguous United States (i.e., those that would occur in the absence of major human or natural disturbances), another that maps the climatic conditions associated with ecosystem function (i.e., "climatic life zones"), and a third that shows the geographic extent of spring snow cover based on satellite imagery. When the team overlaid their historical wolverine records on these maps, a fresh interpretation of wolverine ecology began to emerge.

It had often been assumed that wolverines were habitat generalists that occupied many different types of terrain. "However, our findings revealed that in the West—where the bulk of historical records originated—they frequented an archipelago of habitat 'islands' at high elevations in the northern Cascade Range, the southern Sierra Nevada, and throughout the Rocky Mountains," Aubry explains. "Virtually all those records were within or near areas with alpine vegetation and climatic conditions." A smattering of historical records cropped up in nonalpine locales such as the Northeast and the northern Great Plains. These, the researchers surmised, probably represented wolverines wandering into those areas from populations in Canada and the Great Lakes region. But significantly, the common denominator for the vast majority of the records was a high probability of persistent snow cover during the wolverine's spring denning period, which typically ends in mid-May. "Spring snow cover was the only habitat feature that fully accounted for the historical distribution of wolverines," Aubry concludes.

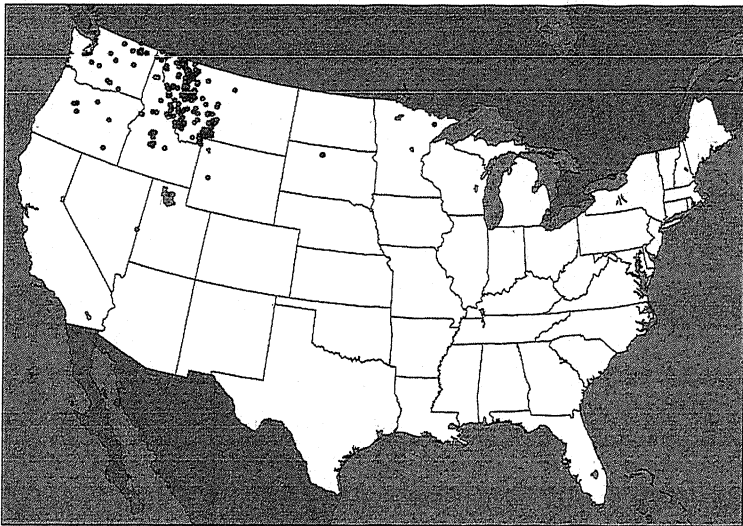
With its compact body, thick fur, and feet optimized for moving across wintry landscapes, the wolverine is well-adapted for life in snowy environments. Females excavate long, complex snow tunnels for reproductive dens, where they give birth to kits and shelter them from predators and harsh weather until weaning time. The close match of wolverine occurrence records with areas covered by snow in the spring offers a convincing explanation for the island-like patterns of habitation in the West, and the accounts of wolverines around the Great Lakes during the 1800s, when a colder climate brought more snow, Aubry says. Conversely, it provides a plausible explanation for the wolverine's historical absence in regions such as the central Great Plains, where food supplies would have been plentiful but enduring spring snow was lacking.

However, Aubry points out, "It's difficult to prove whether an absence of occurrence records represents a real gap in wolverine distribution, or simply an area where the historical record was poorly documented." Although previous distribution maps had showed wolverines occurring throughout the Cascade Range and Sierra Nevada in all three Pacific States, Aubry's team found compelling evidence of their historical presence only in Washington's northern Cascades and the southern Sierras in California.

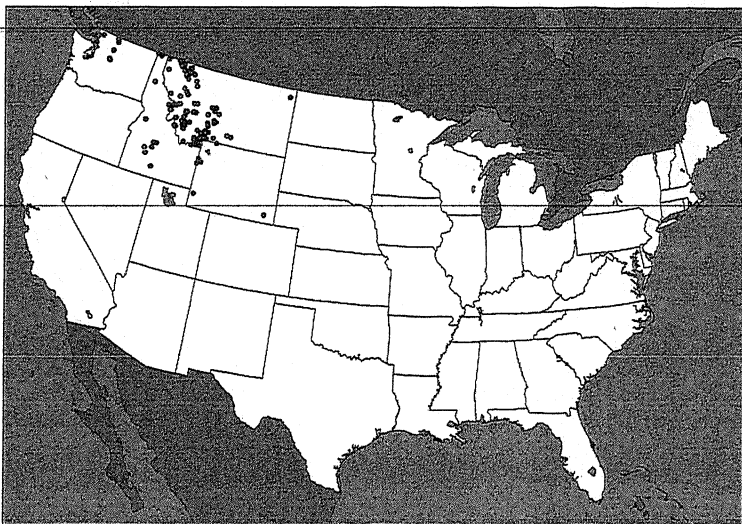
To investigate this apparent gap in wolverine distribution in the Pacific States, the researchers compared DNA samples from California wolverines to samples from outside the golden state. "The genetic results showed that the gap was real. Wolverines that once occupied the southern Sierra Nevada were genetically distinct from all other North American populations, and had been isolated for 2,000 to 10,000 years. Apparently, the geographic extent of suitable wolverine habitat in the intervening area is inadequate to support resident wolverine populations," Aubry says. "Populations that once occurred in California, Colorado, and Utah were probably extirpated by 1930 owing to low or nonexistent immigration from other populations, combined with high levels of human-caused



Historical wolverine locations, 1827 to 1960.



Recent wolverine locations, 1961 to 1994.



Current wolverine locations, 1995 to 2005.

mortality from trappers, hunters, and predator-control programs using poisoned baits,” he concludes.

In the contiguous United States, wolverines currently occur only in northern Washington, northwestern Montana, south-central Idaho, and northwestern Wyoming. About 15 years ago, wolverines reappeared in the north Cascades, where they hadn’t been documented in decades, suggesting that the area had been colonized from another population. In response, Aubry initiated the first radio-telemetry study of wolverines conducted in the Pacific States. Since 2005, Aubry’s field crew has captured and tracked five wolverines, including a pregnant female. The telemetry data show that the animals are residents, not Canadian wanderers—a promising sign. “With human-caused mortality no longer a major threat, there are good reasons to hope that wolverines are taking their place again in Washington’s wilderness areas,” Aubry says.



John Rohrer

Researchers put a radio collar on a temporarily sedated wolverine in northern Washington to learn about the species’ current range in the contiguous United States.

THE IMPORTANCE OF SPRING SNOW COVER

The researchers found further proof of the critical importance of spring snow cover to wolverines in studies that considered an even wider swath of the species’ habitat. A team led by Jeff Copeland developed a finer-scale map of snow cover from mid-April through mid-May (the latter portion of the wolverine’s denning period) covering their entire circumboreal range, and compiled precise location data for 553 wolverine reproductive dens in North America and Scandinavia. When the two maps were overlaid, more than 98 percent of the dens corresponded with areas of spring snow cover.

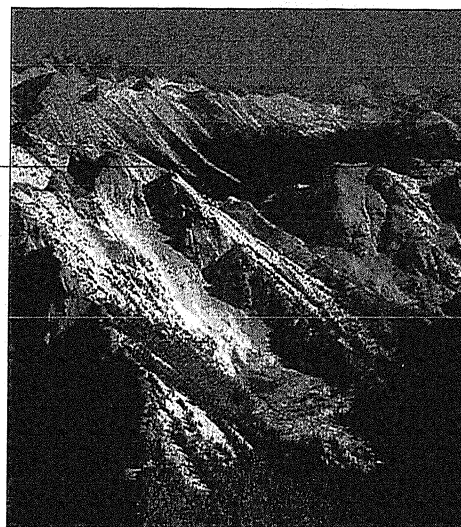
These findings reaffirmed that female wolverines are tied to snow-covered terrain for reproduction, but it was not yet clear whether other members of the population were also restricted to that terrain during winter, or whether wolverines frequented other habitat types during the snow-free months. To investigate these questions, the team scrutinized radio-telemetry data for about 120 wolverines in the northern Rockies, British Columbia, and the north Cascades. “To our surprise we found that wolverines stayed in or near the areas defined by spring snow cover 95 percent of the time, regardless of season. This included males, nonreproductive females,

and juveniles, as well as denning females,” Aubry says. In addition, a team led by Mike Schwartz conducted genetic analyses of Rocky Mountain wolverines to identify areas where gene flow occurs; their results showed that wolverines also use areas with spring snow cover as dispersal pathways. “Thus, if a wolverine needs to get from point A to point B, but there’s a warm, dry valley in between, it will remain in cooler conditions at high elevations and go around the valley, rather than through it,” Aubry explains.



John Rohrer

Female wolverines excavate long snow tunnels where they give birth and raise their kits. This denning period generally occurs between February and May.



Scott Fritkin

Radio-telemetry data showed that wolverines will go around a valley rather than through it, presumably preferring the cooler, high-elevation conditions.

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.

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:

- Aubry, K.B.; McKelvey, K.S.; Copeland, J.P. 2007. *Distribution and broadscale habitat relations of the wolverine in the contiguous United States*. Journal of Wildlife Management. 71: 2147–2158.
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- Schwartz, M.K.; Copeland, J.P.; Anderson, N.J. [and others]. [In press]. *Wolverine gene flow across a narrow climatic niche*. Ecology.
- Ruggiero, L.F.; Aubry, K.B.; Buskirk, S.W. [and others], tech. eds. 1994. *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the Western United States*. Gen. Tech. Rep. RM-GTR-254. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station.

Dan Russell

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United States
Department of
Agriculture

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General Technical
Report RM-217



Management Recommendations for the Northern Goshawk in the Southwestern United States



Fig 9 - pg 22

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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
S/F nest BA-140
(pg 14)

Smag should be 18"
log should be 12"
22- then from below
in nest area
few on

Great hearts 79
Saw all nest - 10
Then nest = 22

A-Guapies - 60

25-
19
Forage - 6 mil
19 mation
010

Diversity = 32

57990-17
PP 08-83

Management Recommendations for the Northern Goshawk in the Southwestern United States

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M. Hildegard Reiser, Richard L. Bassett, Patricia L. Kennedy,
Douglas A. Boyce, Jr., Greg Goodwin, Randall Smith, and E. Leon Fisher**

**Rocky Mountain Forest and Range Experiment Station and
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¹ Author affiliations are listed in Appendix 6.

² The Rocky Mountain Station is headquartered in Fort Collins, Colorado, in cooperation with Colorado State University; the Southwestern Region is headquartered in Albuquerque, New Mexico.

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VEGETATIVE STRUCTURAL STAGES:
Successional stages for a mixed-species forest ecosystem

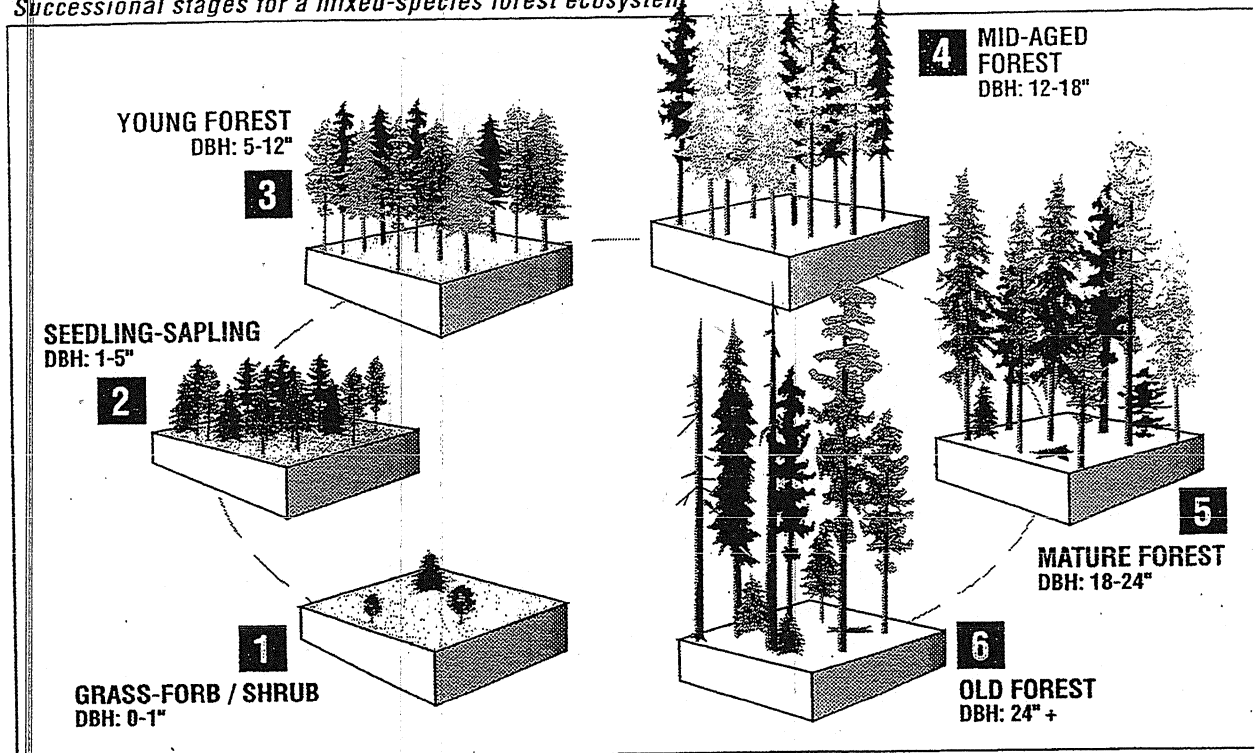


Figure 1. Forest vegetation structural stages and their associated diameter breast height (DBH) ranges.

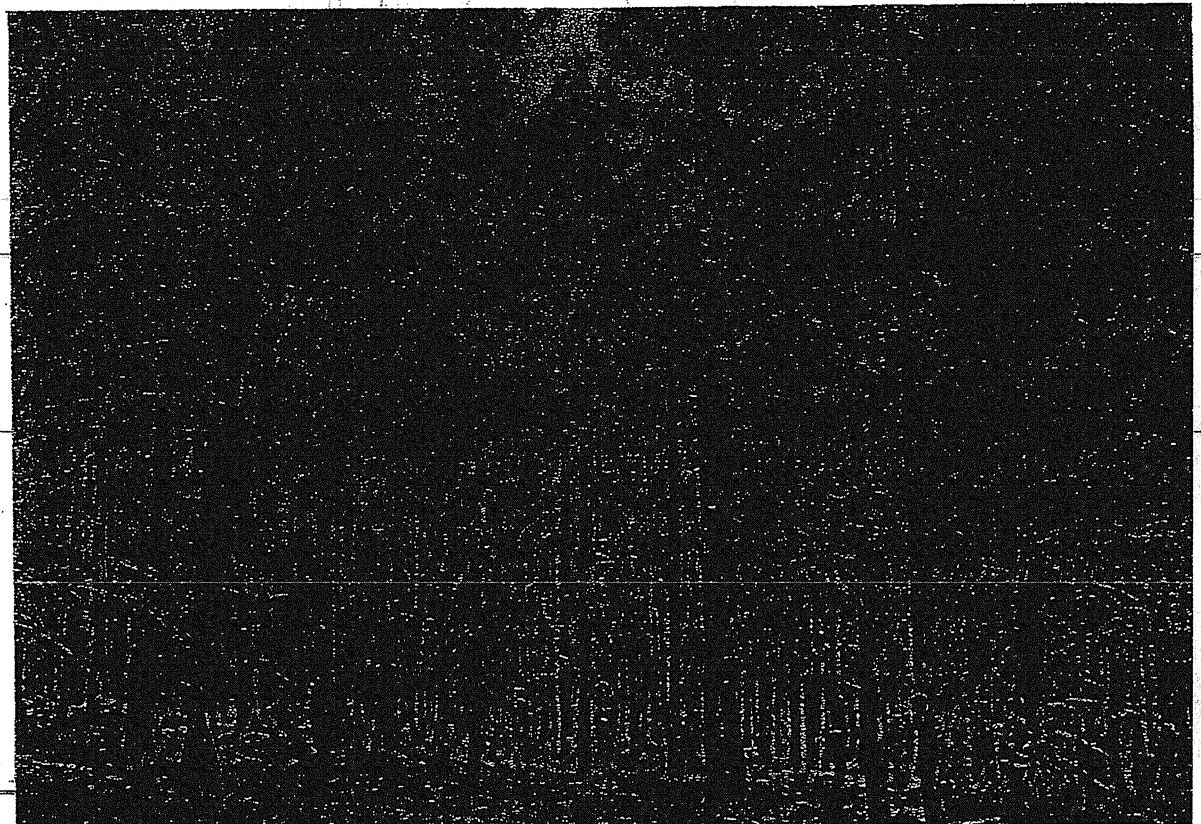


Figure 2. Dense "thicket" of small-diameter trees.

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					
		Post Fledging-Family Area			Foraging Area		
		Ponderosa Pine	Mixed-Species	Spruce-fir	Ponderosa Pine	Mixed-Species	Spruce-fir
VSS distribution ^b							
grass/forb/shrub VSS 1 (%)	0 ^c	10 ^c	10 ^c	10 ^c	10 ^c	10 ^c	10 ^c
seedling-sapling VSS 2 (%)	0	10	10	10	10	10	10
young forest VSS 3 (%)	0	20	20	20	20	20	20
mid-aged forest VSS 4 (%)	0	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+	60+	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 stems 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.

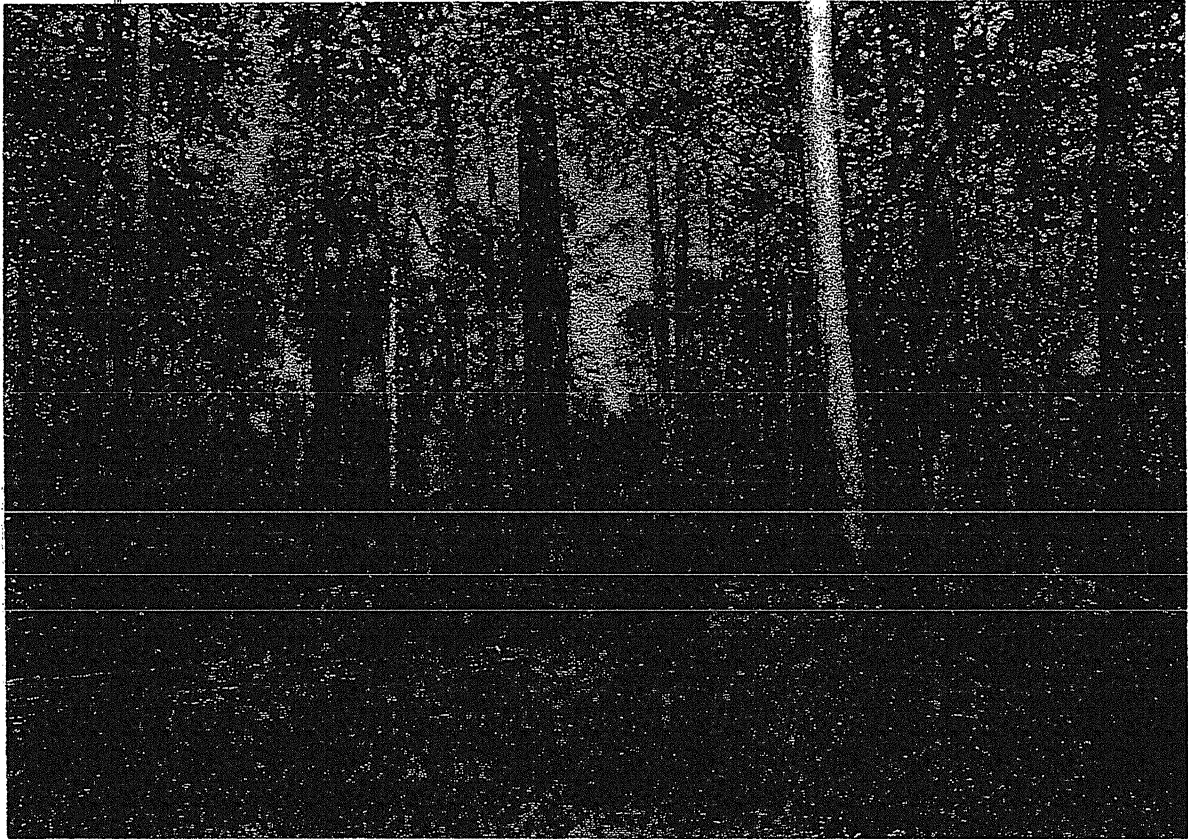


Figure 5. Because of visual limitations in dense forest environments, an open understory enhances detection and capture of prey by goshawks.

downed logs, woody debris, large trees, openings, herbaceous and shrubby understories, and an intermixture of various forest vegetative structural stages. Prey populations within goshawk foraging areas will be abundant and sustainable when:

- 1) the specific habitat attributes are provided,
- 2) forests contain large trees and have relatively open tree understories,
- 3) forest openings are small (1/3 - 2 acres) to medium (2-4 acres) in size,
- 4) patches of dense, mid-aged forests are scattered throughout, and
- 5) the majority of forests are in the "mid-aged," "mature," and "old" structural stages.

Present Forest Conditions

Southwestern forests have been altered from pre-settlement conditions by fire suppression, timber harvesting, livestock grazing, mining, and recreational uses. Prior to fire suppression in the western United States, ponderosa pine forests were burned by low-intensity surface fires at 2- to 15-year intervals. Fires burned at lesser frequencies in

mixed-species forests (5-22 years). These fires maintained forests that were relatively open and dominated by mature trees by regularly burning and killing small trees. In spruce-fir forests, fire intervals were much longer (60-400 years) and fires were often catastrophic, stand-replacing events.

Habitat changes resulting from fire suppression in ponderosa pine and mixed-species, and to a lesser extent spruce-fir forests, are:

- 1) the replacement of open, single-storied stands by dense multistoried stands through tree regeneration,
- 2) loss of natural openings by tree invasion, and
- 3) changes in the abundance and composition of plant species in both the understory and overstory due to plant succession.

Accumulated fuels and dense forest conditions resulting from fire suppression have also increased the potential loss of goshawk habitat through catastrophic wildfire and epidemic infestations of insects and diseases. Increased shading from the dense regeneration has also reduced herbaceous and shrubby understories that provide important foods and cover for goshawk prey. Livestock and wildlife

Executive Summary

The northern goshawk (*Accipiter gentilis atricapillus*) (hereafter called the "goshawk") is the largest North American member of the genus *Accipiter*, which includes both the sharp-shinned hawk (*Accipiter striatus*) and the Cooper's hawk (*Accipiter cooperii*). It breeds in coniferous, deciduous, and mixed forests throughout much of North America.

The goshawk is a forest habitat generalist that uses a variety of forest types, forest ages, structural conditions, and successional stages. It preys on small- to medium-sized birds and mammals (robins and chipmunks to grouse and hares), which it captures on the ground, in trees, or in the air. A single goshawk may consume one-to-two prey per day.

The principal forest types occupied by the goshawk in the Southwest are ponderosa pine, mixed-species, and spruce-fir. There is a concern that populations and reproduction of the goshawk are declining in these forests and elsewhere in the western United States. These declines may be associated with forest changes caused by timber harvesting. However, fire suppression, livestock grazing, drought, and toxic chemicals may be involved. Because of the concerns over the effects of timber harvesting, the goshawk was listed as a "sensitive species" by the Southwestern Region of the Forest Service, U.S. Department of Agriculture in 1982.

The Northern Goshawk Scientific Committee

The Northern Goshawk Scientific Committee (GSC) was established by the Regional Forester of the Southwestern Region in the fall of 1990. Its charter was to develop a credible management strategy to conserve the goshawk in the southwestern United States. This report describes the process used, findings, and recommendations of the scientific committee. In developing the recommendations, we used available information on goshawk biology, behavior, diet, and habitat. Information about goshawk foraging habitat was augmented with information on the habitat and foods of its main prey species. From this the GSC developed a set of "desired forest conditions" that, in their best estimate, will sustain goshawk populations in the Southwestern Region.

Because information on goshawk biology is limited, and our ability to produce and sustain certain forest conditions over long periods is unknown, the

development of the "desired forest conditions" for the goshawk and its prey required certain assumptions:

- 1) goshawks and their prey populations are limited by the availability of their foods and habitats,
- 2) the availability of abundant, sustainable prey populations reduces the probability that food is limiting,
- 3) extreme fluctuations of goshawk populations caused by changes in the abundance of one or more prey will be dampened when a wider variety of prey species are available,
- 4) the foods and habitats of goshawk prey in southwestern forests are similar in adjacent regions, and
- 5) the forest attributes and age-classes of southwestern forests described herein can be sustained with scientific management.

These assumptions reveal areas where research is needed on goshawk and forest ecology.

The following are key concepts fundamental to the GSC recommendations:

- Forests within goshawk nesting home ranges should be an interspersed mosaic of structural stages — young to old forests — to increase the diversity of habitat for goshawks and their many prey species. Six vegetation structural stages (VSS) were used to describe regeneration, growth, and development of forests in the Southwest (Fig. 1). The proportions of the VSS and their interspersion in the forest is how the GSC described the forest mosaic.
- The extent to which southwestern forests were modified by Native Americans before European settlement is not well known. Since European settlement, management practices (such as timber harvesting, livestock grazing, and fire control) have changed the structure and species composition of forests. Today, much forested area consists of dense "thickets" of small-diameter trees (Fig. 2). Forests containing these thickets are prone to catastrophic, tree-killing fire, and insect and disease outbreaks. Because of inter-tree competition for moisture, nutrients, and light, these thickets will not mature into large trees. To accelerate the

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Components of the Nesting Home Range

development of mature forests and large trees, tree cutting and prescribed fire should be used to thin forest stands, concentrating growth on the remaining trees.

- Large trees, snags, and large downed logs provide important habitats for many plants and animals, and provide organic matter to the soil resource. Every acre of a goshawk nesting home range should contain a few large trees in clumps that are never removed. These trees live out their lives, die (become snags), fall, and decompose.
- Forest regeneration, growth, and development varies among locations because site specific productivity differs greatly throughout the Southwest. Therefore, no single management prescription is likely to develop or sustain the desired forest conditions on all sites within a landscape. In fact, the desired forest conditions may not be attainable on sites with low productivity, and may be easily attained on sites with high productivity.

Three components of a goshawk's nesting home range (about 6,000 acres) were identified: nest area, post fledging-family area (PFA), and foraging area. The size of these home range components has been determined from behavioral and radio-telemetry studies of goshawks.

The nest area (approximately 30 acres), which may include more than one nest, is typically located on a northerly aspect in a drainage or canyon, and is often near a stream. Nest areas contain one or more stands of large, old trees with a dense canopy cover (Fig. 3). A goshawk pair occupies its nest area from early March until late September. The nest area is the center of all movements and behaviors associated with breeding from courtship through fledging. Most goshawks have two to four alternate nest areas within their home range; alternate nest areas may be used in different years, and some may be used for decades.

The post fledging-family area (PFA) (approximately 420 acres) surrounds the nest area. Because of its size, it typically includes a variety of forest types and conditions. The PFA appears to correspond to the territory (defended area) of a

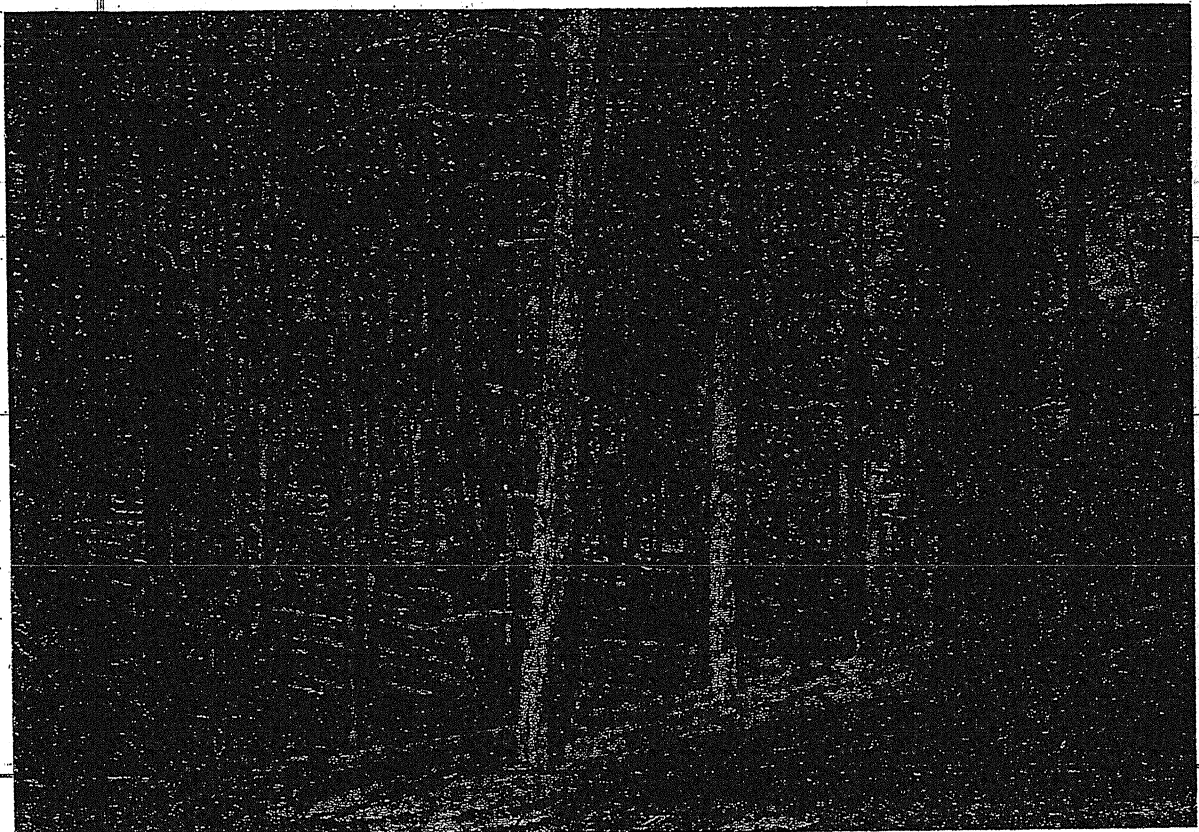


Figure 3. Nest areas contain one or more stands of large, old trees with a dense canopy.

PFA

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goshawk pair, and represents an area of concentrated use by the family from the time the young leave the nest until they are no longer dependent on the adults for food (up to two months). These areas are important for fledglings; they provide hiding cover and prey on which to develop hunting skills. PFAs have patches of dense trees, developed herbaceous and/or shrubby understories, and habitat attributes (snags, downed logs, small openings) that are critical for many goshawk prey (Fig. 4).

The foraging area is approximately 5,400 acres in size, and surrounds the PFA. Hunting goshawks evidently use available habitats opportunistically. This opportunism suggests that the choice of foraging habitat by goshawks may be as closely tied to prey availability as to habitat structure and composition. Goshawks hunt from tree perches by scanning lower portions of the forest (ground, lower canopy) for prey. Because of visual limitations in dense forest environments, an open understory enhances detection and capture of prey (Fig. 5). Raptor (hawks, falcons, owls) populations are often limited by availability and abundance of their prey. The recommendations presented here are based on information available on how foraging goshawks use

their habitat, and was supplemented with information on the habitats, foods, and cover of important goshawk prey.

Goshawk Prey

A comparison of goshawk diets from disparate areas within North America showed that, while as many as 50 species are eaten, about 20 are common in the diets. Fourteen species were important in the diet of southwestern goshawks. Information on the distribution, habitat, special habitat needs, home range size, and populations of these 14 prey species were gleaned from the literature. A synthesis of this information provided a set of "desired forest conditions" that would result in sustainable populations of each prey. Because no single prey species is likely to be abundant enough to support goshawks, especially during the winter and extreme environmental fluctuations (periods of drought), habitats for and populations of all 14 prey are necessary.

1/ Release
2/ Assess
3/ Review
4/ Options

Selected goshawk prey include squirrels, rabbits, woodpeckers, jays, and grouse. Specific habitat attributes used by these species include: snags,

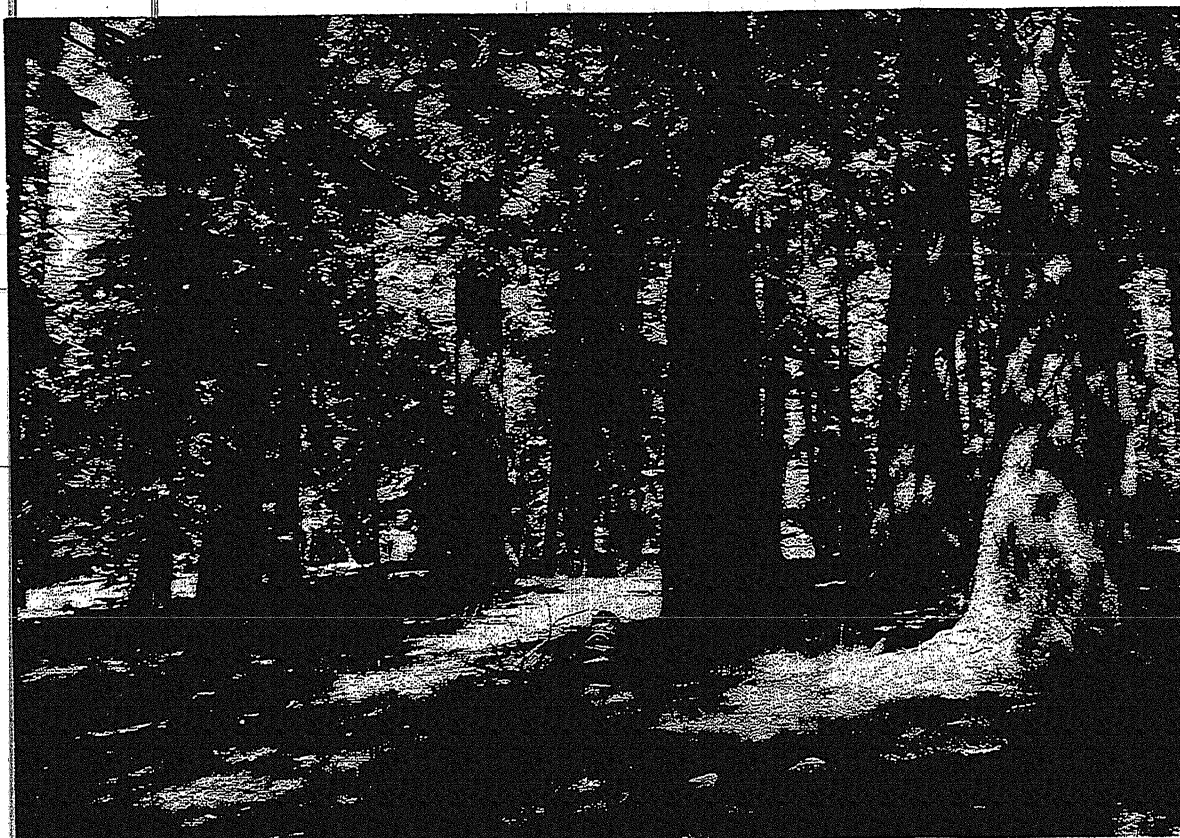


Figure 4. PFAs have patches of dense trees, developed herbaceous and/or shrubby understories, and habitat attributes (snags, downed logs, small openings) that are critical for many goshawk prey.



Figure 5. Because of visual limitations in dense forest environments, an open understory enhances detection and capture of prey by goshawks.

downed logs, woody debris, large trees, openings, herbaceous and shrubby understories, and an intermixture of various forest vegetative structural stages. Prey populations within goshawk foraging areas will be abundant and sustainable when:

- 1) the specific habitat attributes are provided,
- 2) forests contain large trees and have relatively open tree understories,
- 3) forest openings are small (1/3 - 2 acres) to medium (2-4 acres) in size,
- 4) patches of dense, mid-aged forests are scattered throughout, and
- 5) the majority of forests are in the "mid-aged," "mature," and "old" structural stages.

Present Forest Conditions

Southwestern forests have been altered from pre-settlement conditions by fire suppression, timber harvesting, livestock grazing, mining, and recreational uses. Prior to fire suppression in the western United States, ponderosa pine forests were burned by low-intensity surface fires at 2- to 15-year intervals. Fires burned at lesser frequencies in

mixed-species forests (5-22 years). These fires maintained forests that were relatively open and dominated by mature trees by regularly burning and killing small trees. In spruce-fir forests, fire intervals were much longer (60-400 years) and fires were often catastrophic, stand-replacing events.

Habitat changes resulting from fire suppression in ponderosa pine and mixed-species, and to a lesser extent spruce-fir forests, are:

- 1) the replacement of open, single-storied stands by dense multistoried stands through tree regeneration,
- 2) loss of natural openings by tree invasion, and
- 3) changes in the abundance and composition of plant species in both the understory and overstory due to plant succession.

Accumulated fuels and dense forest conditions resulting from fire suppression have also increased the potential loss of goshawk habitat through catastrophic wildfire and epidemic infestations of insects and diseases. Increased shading from the dense regeneration has also reduced herbaceous and shrubby understories that provide important foods and cover for goshawk prey. Livestock and wildlife

browsing and grazing have accentuated this loss. In addition to these changes, timber harvesting, which began in the 1800s, has focused on large trees, resulting in few remaining mature and old forests and associated habitat attributes.

Management Recommendations

The present conditions in southwestern ponderosa pine and mixed-species forests reflect the extent of human interference with natural processes. Given the improbability of returning to the previous frequencies of natural disturbances, some active management (mainly thinning and prescribed fire) will be necessary to produce and maintain the desired conditions for sustaining goshawks and their prey. In some spruce-fir forests, natural processes are still functioning and little or no management may be necessary to maintain the desired conditions.

These recommendations were specifically designed to provide breeding season habitat for the goshawk and its prey. It is not known whether goshawks in the Southwest winter on their nesting home ranges; if they do winter there, then these recommendations will provide habitat and food year-round.

Nest Areas (30 acres each)

Three suitable nest areas should be maintained per home range. In addition, three replacement nest areas per home range should be in a development phase, using intermediate treatment and prescribed fire. Suitable areas may be lost because of insect epidemics, catastrophic fire, or other factors. Nest areas are typified by one or more stands of mature or old trees and dense forest canopies. No adverse management activities should occur at any time in suitable nest areas. Desired forest conditions for the nest stands and management recommendations for maintaining and developing nest stands within nest areas are presented in Tables 1 and 2.

Post Fledging-Family Areas (PFA) (420 acres)

The PFA contains a variety of forest conditions and prey habitat attributes. Interspersed small openings, snags, downed logs, and woody debris are critical PFA attributes. To sustain the desired canopy cover, size of trees, and the specified portions of different forest ages within the PFA, regeneration of 10 percent of the PFA may be required every 20 years. Other management tools, such as prescribed fire and removing understory trees, are suggested for sustaining other critical elements of goshawk habitat

(Table 2).

Small openings in the forest are desired habitat for some prey species and are required for forest regeneration (Fig. 6). If forested openings are 1 acre or greater in Ponderosa pine and mixed species then 3 to 6 large mature and/or reserve old trees per acre should be left in groups. If spruce-fir forest openings are 0.5 acres or greater, a group of 6 reserve trees are required per 0.5 acres. Reserve trees are not necessary in smaller openings; this component can be met in adjacent forested areas. Ponderosa pine and other seral conifers can be planted, and, depending on forest type, aspen and oak regeneration are encouraged. Snags, downed logs, and woody debris should be present throughout the PFA.

All management activities in the PFA should be limited to the period from October through February. Prescribed burning is the preferred method for management of woody debris. Thinning from below (removing understory trees) is preferred for maintaining desired forest structures, and a variable spacing of trees is preferred for developing group trees with interlocking crowns. Road densities should be minimized, and permanent skid trails should be used in lieu of permanent roads. Forage utilization should average 20 percent by weight and should not exceed 40 percent in any area to maintain grass and forb layer. Browse utilization should average 40 percent by weight (Table 2). These recommendations are designed to provide foods (leafy material, berries) and cover for goshawk prey.

Foraging Area (5,400 acres)

Both the desired conditions and the management recommendations for the foraging area are similar to the PFA. The distribution and proportion of vegetative structural stages and the requirements for habitat attributes such as reserve trees, snags, and downed logs are the same as the PFA. Because the foraging area need not provide hiding cover for fledgling goshawks, a more open canopy is preferred -- 40 percent in the mid-aged forests and 40 to 60 percent in the mature and old forests, depending on the forest type. Openings (up to 4 acres), for herbaceous and shrubby understory development and tree regeneration, are desired in ponderosa pine and mixed-species forests; smaller openings are desired in spruce-fir forests (Table 1). Specific management recommendations to obtain the desired conditions for the foraging area are identical to the PFA (Table 2).

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Appendix 1. Description of ponderosa pine, mixed-species, and spruce-fir forest cover types

Ponderosa Pine Forest Cover Type

Ponderosa pine (*Pinus ponderosa* var. *scopulorum*) is one of the most widely distributed forest cover types in the western United States (Table 1). Ponderosa pine is found in pure stands as a climax species or in mixed-species stands as a seral species. For the most part, seed production of ponderosa pine is predictable (Table 2). In a climax situation, natural regeneration of ponderosa pine

establishes best on drier sites with some canopy cover. In a seral situation, seedlings establish readily in small openings on more moist sites. Ponderosa pine is a moderately shade-intolerant species, requiring nearly full sunlight for establishment and growth.

Seedling establishment can be expected to occur within 10 years after opening the canopy and forest floor disturbance. Seedlings develop best under partial shade.

Table 1. Acres of reserved and nonreserved timberland on Southwestern National Forests and the proportion of nonreserved acres by forest cover types.¹

Forest Cover Type	Percent nonreserved	National Forest Timberland, Acres		
		New Mexico	Arizona	Total
Ponderosa Pine	73.6	1,639,548	2,212,420	3,851,968
Mixed-species*	22.9	946,516	253,322	1,199,838
Spruce-fir	3.5	105,444	76,671	182,115
Total nonreserved acres	100.0	2,691,508	2,542,413	5,233,921
Total reserved acres		<u>1,240,722</u>	<u>1,404,642</u>	<u>2,645,364</u>
Grand total		3,932,230	3,947,055	7,879,285

* Includes Douglas-fir, limber pine, white fir, spruce, other softwoods, and aspen forest types.

¹ Conner et al. 1990, Van Hooser et al. unpublished.

Table 2. Heavy cone crop interval years and optimum age of seed production for tree species in ponderosa pine, mixed-species, and spruce-fir forests.

Species	Interval of Heavy Crop (Years)	Age of Optimum Seed Production	Reference
Blue spruce	2-3	50-150	Fechner 1990
Corkbark fir	3-4	150-200	Alexander et al. 1990
Douglas-fir	7	200-300	Hermann and Lavender 1990
Engelmann spruce	2-5	150-250	Alexander and Shepperd 1990
Gambel oak	4-5	Sprouts vegetatively	Daniel 1980
Limber pine	2-4	Unknown	Steele 1990
Ponderosa pine	3-4	60-160	Minore 1979, Oliver & Ryker 1990
Southwestern white pine	3-7	Unknown	Krugman & Jenkinson 1974
Subalpine fir	3-4	150-200	Alexander et al. 1990
White fir	3-9	Unknown	Laacke 1990
Aspen	NA ¹	Suckers vegetatively	Perala 1990

¹ NA: Not applicable.

Appendix 2. Vertebrates in the diets of nesting northern goshawks from various locations in North America

Species are listed in approximate order of decreasing size and potential contribution to the biomass consumed by the goshawks.

Species ¹	Number of Prey (% in the diet)				
	Schnell 1958 ²	Meng 1959 ³	Reynolds & Meslow 1984 ⁴	Mannan & Boals 1990 ⁵	Kennedy 1991 ⁶
Great-horned owl			1 (0.5)		
Mallard	3 (4)		2 (1)		
Cat (<i>Felis</i> spp.)					1 (1)
Black-tailed jackrabbit				2 (1)	
Snowshoe hare	1 (1)		24 (1)		
Blue grouse			5 (2)		
Unknown grouse			1 (0.5)		
Cottontails		7 (4)	3 (1)	16 (12)	25 (20)
Gray squirrel		4 (2)	5 (2)		
Common raven					3 (3)
Prairie falcon					1 (1)
Ruffed grouse		5 (3)	2 (1)		
Pigeon (<i>Columba</i> spp.)	1 (1)				2 (2)
Common crow		83 (45)			
Tassel-eared squirrel				7 (5)	9 (9)
Cooper's hawk			1 (0.5)		2 (2)
Bushy-tailed woodrat			1 (0.5)		
Pileated woodpecker			1 (0.5)		
Rock squirrel				3 (2)	
Tree squirrel spp.					7 (7)
Belding's ground squirrel	3 (3)		4 (2)		
Woodrat spp.			1 (0.5)		
Mountain quail	1 (1)		9 (4)		
Dusky footed woodrat			1 (0.5)		
Squirrel (<i>Tamiasciurus</i> spp.)	5 (6)	58 (31)	13 (6)	2 (1)	3 (3)
Black-billed magpie			1 (0.5)		
Screech owl			1 (0.5)		
Northern flying squirrel			15 (7)		
Mantled ground squirrel	6 (7)		17 (7)	21 (16)	2 (2)
Northern flicker			15 (7)	5 (4)	15 (14)
Townsend's ground squirrel			2 (1)		
Mourning dove			7 (3)		1 (0.7)
American kestrel		3 (2)			1 (1)

Continued on next page.

Cottontails (*Sylvilagus* spp.)

Desert Cottontail (*S. auduboni*)
Eastern Cottontail (*S. floridanus*)
Mountain Cottontail (*S. nuttalli*)

Due to their medium size (14.8-15.6 inches in length and average weight of 3.3 pounds) and widespread distribution, several species of cottontails are common prey throughout the range of the goshawk (Reynolds and Meslow 1984, Reynolds 1989, Kennedy 1991). Mannan and Boal (1990) observed 16 cottontail prey deliveries (11.9%) to nests in northern Arizona. Twenty percent of prey remains collected at goshawk nests in north-central New Mexico were cottontails (Kennedy 1991). Because it is difficult to distinguish among cottontail species in dietary remains and because of differences in the habitats occupied, it is difficult to determine which species may be important prey of goshawks in the Southwest. Therefore the following management recommendations are a composite of the habitat needs of these species. These species are segregated along habitat-elevational gradients from grasslands to spruce-fir. During the nesting season, when goshawks are in coniferous forests, the eastern and mountain cottontails are more likely to occur in goshawk diets. During the winter, desert cottontails could also be consumed by goshawks in piñon-juniper woodlands and other low elevation habitats. Key recommendations for ponderosa pine, mixed-species, and spruce-fir forests are based on the cottontail species that predominate these plant communities.

Distribution

All three species of cottontail occur in the Southwest. Desert cottontails are widespread and abundant in low- and mid-elevation habitats throughout the Southwest. Eastern cottontails are found in mountainous areas of southwestern New Mexico and southeastern Arizona (Findley et al. 1975, Cockrum 1982, Findley 1987). Mountain cottontails are found in mountainous regions north of the Mogollon Rim (Cayot 1978, Cockrum 1982). In New Mexico, mountain cottontails occur in the Jemez, San Juan, Sangre de Cristo, and Chuska Mountains (Findley 1987).

Habitat

According to Findley (1987), desert cottontails are primarily located in grassland, shrubland, and woodland habitats in the upper Sonoran and Sonoran zones in New Mexico. In Arizona, desert cottontails are found at elevations below 6,000 feet in brushy

areas as well as xeric forest habitats (e.g., ponderosa pine) (Cockrum 1982, Ffolliott 1990).

In New Mexico, the eastern and mountain cottontails chiefly inhabit montane forests, from lower elevation ponderosa pine forests to higher elevation mesic forests (mixed-species, spruce-fir) (Findley 1987). According to Cockrum (1982), eastern cottontails in Arizona are restricted to oak woodlands associated with riparian habitats.

In Colorado, mountain cottontails decreased in abundance as elevation increased from 6800 feet to 8900 feet (Cayot 1978). At higher elevations, mountain cottontail abundance tended to be greater on southeast aspects where ponderosa pine was more common and bitterbrush (*Purshia tridentata*) ground cover increased to 50% (Cayot 1978). Prevalence of bare ground, common juniper (*Juniperus communis*), and downed timber were negatively associated with mountain cottontail abundance.

In southern British Columbia, within the ponderosa-pine-bunchgrass plant association, which includes grassland, sagebrush, riparian, ponderosa pine parkland, open Douglas-fir forest, and lodgepole pine forest, mountain cottontails preferred habitats dominated by sagebrush (Sullivan et al. 1989).

Food

Cottontail diets vary greatly among species, geographic region, and availability of palatable plants (Chapman et al. 1982). In a given geographic area, cottontails may eat more than 100 plant species but food preferences vary locally (DeCalesta 1971). A wide variety of vegetation is acceptable, provided basic nutritional requirements are met (Chapman et al. 1982). Herbaceous vegetation is typically selected during the growing season, and the bark, buds, and twigs of woody vegetation are consumed during the remainder of the year. Use of woody vegetation during the fall and winter is assumed to relate to reduced availability of herbaceous vegetation and not a preference for woody vegetation (Chapman et al. 1982). In southern portions of the Southwest where winter climates are mild, herbaceous vegetation may provide an adequate year-round source of food (Allen 1984).

Special Habitat Needs

All three species of cottontail prefer habitat with well-developed shrub and herbaceous understory for food and escape cover (Cayot 1978, Pils et al. 1981, Allen et al. 1982). Most eastern cottontail nests are located in grass cover, dense brush, and downed logs (Allen 1984). No information on nest sites for the desert and mountain cottontail was available. However, mountain cottontails preferred crevices in

outcrops as daytime retreats in a sagebrush-juniper habitat in Oregon (McKay and Verts 1978). McKay and Verts (1978) concluded that mountain cottontail abundance in this habitat type was strongly influenced by the abundance of these daytime retreats. Conversely, in Colorado, Cayot (1978) found no relationship between the presence of rocks and mountain cottontail abundance.

Home Range

Home ranges of 25 radio-tagged eastern cottontails in a 14-acre woodlot in southwestern Wisconsin varied by season, sex and individual (Trent and Rongstad 1974). Adult male home ranges increased from an average of 6.8 acres in the spring to an average of 9.9 acres in early summer, and had decreased significantly to an average of 3.8 acres by late summer. Adult female home ranges were largest (average 4.3 acres) in spring, then decreased significantly to an average of 2.1 acres in early summer and remained about this size until mid-January. Additionally, fall home range sizes of four juveniles did not differ from 10 adults, and showed no difference according to sex (Trent and Rongstad 1974).

No information was found on home range sizes for desert and mountain cottontails.

Population

Cottontail populations are characterized by substantial seasonal and annual fluctuations. Scribner and Warren (1990) estimated winter densities of two populations of eastern cottontails in Texas to be 3.2 and 4.9 individuals per acre. After reproduction and juvenile dispersal, the densities in these two areas peaked at 10.9 and 11.3 individuals per acre, respectively.

Fall density of eastern cottontails in southwestern Wisconsin woodlots was estimated to be 3.6 individuals per acre (Trent and Rongstad 1974). In this population, annual survivorship was estimated to range between 0.15 and 0.2 depending on the estimation technique. Fall and winter eastern cottontail densities over a 5-year period in southern Wisconsin ranged from 7.4 to 23.7 individuals per acre and 3.7 to 12.9 individuals per acre on controlled and experimentally managed 50-acre woodlots, respectively (Pils et al. 1981).

Population densities of mountain cottontails in ponderosa pine-bunchgrass habitat in southern British Columbia varied annually, from 0.09 to 0.17 individuals per acre. McKay and Verts (1978) found that mountain cottontail population densities varied annually from 0.03 to 1.03 individuals per acre in shrub-juniper habitat in central Oregon.

Management Effects

Although habitat studies have not been conducted on eastern cottontails in the southwestern U.S., there is evidence that small areas of brush (in strips 100 feet wide) can provide cottontail habitat (Allen et al. 1982). Additionally, they suggest establishing brush areas at the edges of fields or meadows and forested areas by felling trees within 30 feet of the edge. However, their results also suggest that narrow brushy field borders may be useless for enhancing cottontail habitat if the adjacent wooded area provides only minimal or poor habitat (e.g. areas lacking in shrub and herbaceous understory for food and escape cover).

The effectiveness of experimental habitat management on eastern cottontail abundance was monitored in southern Wisconsin woodlots between 1976-1979 by Pils et al. (1981). Brush pile construction, planting of shrubs, and sowing of food patches were the primary management practices implemented in a 50.2-acre experimental woodlot to increase cottontail numbers. Half-acre portions of the woodlot were clearcut to encourage early successional growth and to construct loose brush piles. They also established food, nesting, and escape cover plots through plowing and disking, planting, mowing, and controlled burning. Cottontail populations were higher on the 50-acre control plot than on the experimental plot during the pre-habitat management and experimental periods. Abundance on both the control and experimental plots showed a downward trend during the 4-year period. Greater vulnerability of experimental populations to hunting because of improved hunter access and less dense total cover were presented as the major reasons habitat management efforts did not result in measurable population increases as compared to the control (Pils et al. 1981). The authors recommended that future habitat management practices should include denser concentrations of brush piles and food patches.

No information was found on specific management recommendations for southwestern populations of any of three cottontails.

Habitat Management Recommendations

The following are composite recommendations for the three cottontail species:

✓ Forest and woodland generalists

- VSS 1, VSS 2, VSS 3, VSS 4, VSS 5, and VSS 6

✓ Nesting

- VSS 3, VSS 4, VSS 5, and VSS 6
- Large downed woody debris, base of snags and rocks important for eastern and desert cottontail. The importance of these

Management Recommendations

attributes for mountain cottontail is unknown.

✓ Foraging

- VSS 1, VSS 2, VSS 3, VSS 4, VSS 5, and VSS 6
- Well developed herbaceous and shrub layers are important
- Downed logs and woody debris are important for escape cover, particularly in areas with poorly developed shrub understory, for desert and eastern cottontail. The importance of these attributes for mountain cottontail is unknown.

✓ Other important habitat attributes

- Small openings or sufficiently open overstories that allow development of herbaceous and shrub layers improves foraging habitat.

✓ Hairy Woodpecker (*Picoides villosus*)

The hairy woodpecker averages 2.2 ounces (Li and Martin 1991) and is approximately 9 inches in length. It is widely distributed throughout forested habitats in the United States, and as a result of its abundance and distribution, regularly occurs in the diet of the goshawk (Reynolds and Meslow 1984, Mannan and Boal 1990, Kennedy 1991).

Distribution

Hairy woodpeckers are year-round residents of nearly all forest types from central Canada to the southern United States (Scott et al. 1977).

Habitat

This species is one of the most common woodpeckers in the Southwest, particularly in riparian habitats and in ponderosa pine, mixed-species, and spruce-fir forests (Hubbard 1978).

Food

Hairy woodpeckers prefer to feed on insects on dead or diseased trees. Approximately 80% of the diet is animal matter -- larval and adult beetles, ants and caterpillars are most frequently eaten. Coleoptera (primarily Buprestidae and Scolytidae beetles) comprised an average of 63.8% of the diets of male and female hairy woodpeckers in California. Hymenoptera (mainly carpenter ants) were the second most common diet item in both sexes (Otvos and Stark 1985). This insectivorous diet was supplemented with fruit, grains, and nuts (Scott et al. 1977). Hairy woodpeckers (both sexes) also fed on seeds of ponderosa pine (Otvos and Stark 1985).

The sexes of this species selected different foraging sites throughout the year (Morrison and With 1987). According to Scott et al. (1977), males foraged in trees away from the nest for large insects (usually borers). Females foraged close to the nest on the surface of trees, shrubs, or on the ground for small insects and plant material.

In the western Sierra Nevada during the breeding season, Morrison et al. (1987) and Morrison and With (1987) found that both sexes of the hairy woodpecker concentrated their foraging activities on trunks of trees at heights from 33 to 39 feet. During the winter, this species forages higher.

In a mixed-conifer area in the Sierra Nevada, Morrison et al. (1986) found that foraging hairy woodpeckers used lower and upper strata of the tree canopy and areas with smaller diameter trees (4-12 inches DBH).

Special Habitat Needs

Live trees in open woodlands with deciduous understory are preferred nesting sites of hairy woodpeckers. This species excavates a nest entrance 1.6 to 1.8 inches in diameter. Because this is the nest cavity size preferred by other cavity nesters such as starlings (*Sturnus vulgaris*), competition for nest sites may occur (Scott et al. 1977).

Hairy woodpeckers will often excavate the nest entrance so it is hidden, such as on the underside of a limb. Nest heights vary from 15 to 45 feet, but are typically 35 feet high. This species will often use the same nest hole for several years (Scott et al. 1977).

Of 8 hairy woodpecker nests located in 3 study areas (ponderosa pine, subalpine fir, and aspen) by Scott et al. (1980), 2 were in aspen snags and 6 were in live aspen trees. Nest heights averaged 33 feet (range 22-50 feet), nest tree heights averaged 59 feet (range 35-70 feet) and nest tree DBH averaged 15 inches (range 10-23 inches) (Scott et al. 1980). Hairy woodpeckers showed a nest site preference for ponderosa pine snags with DBH of >20 inches in an area of the Santa Catalina Mountains in southeastern Arizona (Horton and Mannan 1988).

In the western Sierra Nevada, hairy woodpeckers showed high use of white fir and ponderosa pine for feeding trees throughout the year (Morrison et al. 1987, Morrison and With 1987). In this area, the hairy woodpecker foraged on live trees and snags with similar frequency, but about 70% of their foraging time was on dead substrate within the tree. The average DBH of the feeding trees was 17.4 inches (Morrison et al. 1987). The feeding trees of males and females did not differ in size during the breeding season, nor did trees used in winter differ from those used in the breeding season (Morrison and With 1987).

height varies from 5 to 7 feet above ground and the same nest is often used repeatedly, although a new cavity is excavated each year. Li and Martin (1991) located 20 nests in the Mogollon Rim country of central Arizona. All were found in aspen trees (20% snags, 25% dead portions of live trees, and 55% in live trees). The average nest tree height was 43.6 feet and the average nest tree DBH was 14.6 inches. Snag densities averaged 2.3 per nest plot (0.1 acre), 1.7 aspen snags and 0.6 conifer snags.

Scott et al. (1980) characterized 6 nests located in 3 forest types (ponderosa pine, subalpine spruce-fir, and aspen) in the Rocky Mountains. Five were in live aspen and 1 in an unidentified conifer snag. The average nest height was 39 feet (25-60 feet), average tree height was 62 feet (45-80 feet), and the average DBH of the nest trees was 16 inches (14-19 inches).

This species regularly uses 1 to 2 trees in its territory for foraging. These feeding trees generally show signs of damage (porcupines, logging) (Scott et al. 1977). Red-naped sapsuckers drilled sap holes in all tree species available in their winter habitat in the Huachuca Mountains, Arizona including: oak (45.7% of sap trees), juniper (4.9% of sap trees), pine (11.1% of sap trees) and a variety of deciduous species (19.8% of sap trees) (Bock and Larson 1986).

Home Range

No home range information was found on the red-naped sapsucker.

Population

McPeck et al. (1987) experimentally doubled the density of snags greater than 3.9 inches DBH and greater than 16.3 feet tall in a hardwood forest in Kentucky, from 60 snags per acre in 1981 to 183 snags per acre in 1983. Snag densities on the control areas averaged 7.3 per acre. Winter densities of sapsuckers were not significantly different between experimental (0.4-1.2 birds per 100 acre) and control (0.4-0.8 birds per 100 acre) forests. McPeck et al. (1987) concluded that no numerical response was observed in winter because:

- 1) the birds did not depend on snags as feeding substrate,
- 2) food was not limiting to these woodpeckers, or
- 3) they fed more heavily on fruits, seeds, and sap.

Management Effects

Due to this sapsucker's preference for aspen nest trees, maintenance or regeneration of aspen is important. Development of oak and other deciduous trees in the understory for feeding and nesting will also benefit the red-naped sapsucker. High snag

densities appear to improve red-naped sapsucker habitat.

Habitat Management Recommendations

- ✓ **Forest generalists (lower elevations), commonly mixed with aspen**
 - VSS 4, VSS 5, and VSS 6
 - Riparian and forests with oak understory very important, particularly in the winter
- ✓ **Nesting**
 - VSS 4, VSS 5, and VSS 6
 - Snags or live decadent trees (wounded, decayed heartwood), especially aspen, very important
 - Nest tree diameter 15-16 inches DBH and 39-44 feet in height
- ✓ **Foraging**
 - VSS 4, VSS 5, and VSS 6
 - Decadent trees (wounded, decayed heartwood) very important
- ✓ **Other important habitat attributes**
 - Snags, especially aspen, are important
 - Downed logs and woody debris are sources of insect food
 - Deciduous understory (aspen, oak) is important for nesting and foraging

Red Squirrel

(*Tamiasciurus hudsonicus*)

(Mount Graham Red Squirrel)

The red squirrel is a small tree squirrel, total length 12-14 inches, weight 0.4-0.5 pounds (Burt and Grossenheider 1964, Hoffmeister 1986). Within certain habitats, the red squirrel is commonly used as prey by the goshawk. Rusch and Meslow in Canada (pers. comm. in Rusch and Reeder 1978) estimated that a total of 306 red squirrels were taken by a pair of goshawks during three breeding seasons, and that goshawks may take a greater number during winter when the variety of prey species is reduced. In the Jemez Mountains of northern New Mexico, the red squirrel comprised 5.6% of 36 prey deliveries to 7 goshawk nests and 17.5% of 63 pellets analyzed from 8 goshawk nests (Kennedy 1991). In eastern Oregon, the Douglas squirrel (*Tamiasciurus douglasi*) comprised 5.7% of the diet of goshawks (Reynolds and Meslow 1984). In northern Arizona, 1.5% of 135 prey deliveries to 7 goshawk nests were red squirrels (Mannan and Boal 1990).

Distribution

This sciurid is a forest-dependent mammal that ranges from Alaska through most of Canada into the hardwood and coniferous forests of the upper midwestern, northeastern, and Appalachian states.

Management Recommendations

The red squirrel also is found throughout the coniferous forest of the Rocky Mountains and south into the mountains and higher elevation plateau areas of Arizona and New Mexico (Martin et al. 1951, Hoffmeister 1986, Sullivan 1990).

Habitat

In the western United States, the red squirrel is found almost exclusively in conifer forests, including spruce-fir, Douglas-fir, and lodgepole pine. Mature stands of conifers are preferred. In the Southwest, Engelmann spruce or a mixture of spruce and Douglas-fir are the most important and commonly inhabited forest types (Vahle 1978). The red squirrel is less common in mixed forests of ponderosa pine and Douglas-fir, and rarely in pure ponderosa pine stands (Rasmussen 1941, Gurnell 1984, Hoffmeister 1986, Sullivan and Moses 1986). However, Uphoff (1990) found that lower elevation mixed-species/deciduous habitat supported high densities of red squirrels. Her study area was located on the Mogollon Rim in central Arizona (elevation 7500 feet). The ridge and drainage system contained a mixture of ponderosa pine, southwestern white pine, Douglas-fir, white fir, and Gambel oak. Riparian understories were dominated by big-toothed maple, quaking aspen, and New Mexican locust.

Food

Conifer seeds are the year-round dietary staple. Some commonly eaten and preferred seeds in the Southwest include Douglas-fir, blue spruce, Engelmann spruce, and white fir (C. Smith 1968, Rusch and Reeder 1978, Gurnell 1984, Hoffmeister 1986, Patton and Vahle 1986, Sullivan and Moses 1986). Ponderosa pine seeds were occasionally noted as being used on the North Kaibab Plateau, Arizona (Rasmussen 1941). Although ponderosa pine seeds had the highest quantity of energy per seed out of 7 species of conifers, they were taken second most frequently in feeding trials (91 of 108 trials = 84%) (C. Smith 1968).

Because seed crops fluctuate widely from one year to the next, cones caches not only provide a stable food source during the following winter, but they may also serve as the primary winter food source through an additional 1 or 2 years of cone crop failure (M. Smith 1968).

Meristematic buds are an important winter and spring food supplement, especially in years when cone crops fail (M. Smith 1968, Rusch and Reeder 1978). Leaf buds were eaten in early July in mixed-species forests in Arizona (Uphoff 1990). Conifer pollen is eaten from late spring to mid-summer depending on tree species. However, pollen is available for only 2 or 3 weeks during this

period.

Fungi are available from spring through fall. Fungi are harvested and placed in forks of tree branches and logs for drying and storage. These stored mushrooms are eaten sparingly throughout the winter (Hatt 1929, C. Smith 1968, M. Smith 1968, Rusch and Reeder 1978). In southern British Columbia, C. Smith (1968) identified 42 species of fungi eaten by red squirrels. Preferred species included those in the genera *Suillus*, *Rhizopogon*, and *Chroogomphus*. In an analysis of 5 red squirrel stomachs from Oregon, Maser et al. (1978) noted that basidiomycetes fungi were taken most frequently and that fungi made up 77% of diet volume. In the Mogollon Rim country of central Arizona, the most common hypergeous fungi gathered by squirrels were *Fistulina hepatica*, *Cortinarius rufolivaccus* and *Pleurotus porrigens* (Uphoff 1990). These fungi were stored in secondary food caches, while hypogeous fungi, such as *Geopora cooperi* and puffballs, would be eaten immediately upon discovery. Fungi were the most commonly eaten summer food by females in central Arizona. This food source was utilized from the beginning of the rainy season in mid-June through September (Uphoff 1990, Reiser pers. obs.).

Red squirrels also eat fruits, seeds, sap, acorns and nuts of angiosperm trees and shrubs (cottonwood, maple, wild rose, blueberry, raspberry, wild strawberry, bracken fern). They also chew on animal bones, and eat insects, soil, and feces (Hatt 1929, Layne 1954, Brink and Dean 1966, C. Smith 1968, M. Smith 1968, Rusch and Reeder 1978, Uphoff 1990). Red squirrels also regularly eat passerine bird eggs (Martin 1988, Uphoff 1990).

Special Habitat Needs

Food caches (middens) are of paramount importance to red squirrels. Without these middens, winter starvation is inevitable (M. Smith 1968, Kemp and Keith 1970). A large centrally-located (primary) midden is the most prominent feature of red squirrel territories. These primary middens, along with several secondary middens, provide the energy requirements of a single squirrel for half of the year (Rusch and Reeder 1978, Gurnell 1984, Patton and Vahle 1986). Cache sites are in moist, shaded areas. At cache sites, groups of mature trees and shading from additional understory and overstory vegetation maintains the humidity necessary to prevent the cones from opening.

These mesic areas also support other foods sensitive to desiccation, such as fungi, conifer buds, grasses, berries, and insects. These foods are important to juvenile red squirrels learning to forage on their own (Uphoff 1990).

Vahle and Patton (1983) found that 90% of 141 cache sites had canopy cover greater than 60%, and received additional shading from surrounding uneven-aged groups of trees. Canopy cover in a 33-foot-radius plot centered on primary middens averaged 89% (n=144) for Mount Graham red squirrels (Mannan and Smith 1991). One or more large (≥ 20 inches DBH) snags, fallen logs, and/or live trees act as support structures for the primary middens (Vahle and Patton 1983). Basal areas at middens in old-growth mixed-species forests were higher (197 square feet per acre) than on randomly chosen sites (142 square feet per acre). Midden sites had more large trees (≥ 20 inches DBH) than non-midden sites. Midden plots (0.1 acre) in the White Mountains contained an average of 3 large, dominant trees (≥ 30 inches DBH) (Vahle and Patton 1983, Patton and Vahle 1986). Mannan and Smith (1991) averaged almost 4 trees (≥ 16 inches DBH) per midden site.

Territory size has been linked with food requirements. The number of cones required to sustain a single red squirrel for a year ranges from 42,000 to 131,000, thus 9 to 25 large, mature, cone-producing trees per territory are necessary (C. Smith 1968, Rusch and Reeder 1978, Gurnell 1984, Patton and Vahle 1986).

In Douglas-fir, 200- to 300-year-old trees are the best seed producers. These old trees may produce 20 to 30 times more seed than trees that are 50 to 100 years old (Hermann and Lavender 1990). White fir begin producing cones around 40 years of age and continue beyond 300 years of age. Dominant trees in the 12 to 35 inch DBH range are the best and most reliable cone producers (Laacke 1990). Engelmann spruce begin to produce abundant cone crops once they have reached a DBH greater than 15 inches, and are 150 to 200 years old. This spruce is a long-lived species that does not fully mature until 300 years of age, and may live upwards of 600 years (Alexander and Shepperd 1990). Blue spruce is also a slow growing, but long-lived species (>600 years). However, its best seed producing years range between 50 and 150 years (Fechner 1990).

Nest trees have crowns that interlock with 2 or more adjacent trees (Vahle and Patton 1983). In a mixed-species forest in Arizona, nest trees averaged 14 inches DBH (3-35 inches). Average distance between nest trees and the primary middens was 15 feet (0-80 feet; 186 nests) (Vahle and Patton 1983). In a mixed hardwood forest in New York, Layne (1954) found leaf nests in trees whose DBH ranged from 4 to 16 inches, and DBH of trees with cavity nests ranged from 12 to 36 inches.

Home Range

Home range estimates for adult red squirrels range from 0.7 to 2.0 acres in a lodgepole pine forest (n=9), from 0.5 to 11 acres in a mixed hardwood-conifer forest (n=13) (Layne 1954, Gurnell 1984). Most researchers report estimates of territory size, and Gurnell (1984) found that territories were about 60% to 100% of the squirrels' home range. In two spruce-fir and hemlock-cedar sites in British Columbia, adult territories were contiguous and non-overlapping and averaged 2.2 acres (10 low elevation sites) to 1.3 acres (5 high elevation sites) (C. Smith 1968). Squirrel home ranges decreased in size as the number of trees greater than 10 inches DBH increased. These territories had the highest densities of cones available to the squirrels (C. Smith 1968). Territories, estimated from observations of 23 marked individuals, in mixed white spruce, black spruce, jack pine, and aspen and poplar forests ranged from 1 to 2 acres (Kemp and Keith 1970). Rusch and Reeder (1978) estimated territories of 0.6 to 1.6 acres in similar habitat. In a low elevation mixed-species/deciduous forest, Uphoff (1990) estimated minimum defended territories of 0.07 acres.

Population

Spring density of adult red squirrels over a 50 year period tended to be similar within a variety of conifer forests: densities averaged 1.1 squirrels per acre in spruce forests, 0.7 in mixed-species forests, and 0.4 in pine forests (Rusch and Reeder 1978, their Table 13). Since these studies spanned 50 years, a wide variety of overwintering conditions and cone production was encountered.

Vahle and Patton (1983) estimated population densities from 0.4 to 1.0 squirrel per acre in old growth mixed-species forests, while Ward (unpublished data) estimated red squirrel densities of 0.03 to 0.32 per acre in mixed-species forests of the Sacramento Mountains, New Mexico. In mixed-species/deciduous drainages, squirrel densities averaged 1.7 per acre in a 45 foot corridor down the center of the drainages (primarily occupied by females). Densities declined to 0.61 squirrel per acre in a corridor located on the upper slopes of drainages, where there were equal numbers of male and female territories. Ridgetops in mixed-species forests were more frequently occupied by males (Uphoff 1990).

Densities in a lodgepole pine forest were estimated at 0.3 adult red squirrels per acre (Gurnell 1984). Squirrels were more abundant in both unthinned and managed young (20 years of age)

Management Recommendations

stands of lodgepole pine, than in thinned (20 year) stands (0.5 versus 0.2 squirrel per acre, respectively). Unthinned young stands had similar densities to mature (110-year-old) stands of lodgepole pine.

In mature stands, 100% of adult females attained breeding condition, while only 56% did so in young stands. Survival was significantly higher in mature stands. Similar densities in young unthinned stands were thus maintained by higher recruitment rates into the young stands (Sullivan and Moses 1986). The suboptimal habitat of the unthinned young stands seemed to serve as a dispersal sink for yearling and young squirrels from the surrounding mature forests (Sullivan and Moses 1986). Red squirrel tracks were generally more abundant in uncut forests than in 1- to 33-year-old clear-cuts (Thompson et al. 1989).

Old-growth forest stands (250-730 yr) of Douglas-fir and western hemlock in the Cascade Range of Washington supported densities of Douglas squirrels that were 3 times higher than in young forest stands (42-165 yr). Young forests were dominated by Douglas-fir. Old-growth forests supported 0.25 squirrels per acre, while the young forest stands supported 0.07 squirrels per acre. Cone crops for both Douglas-fir and western hemlock were rated "very poor" and "extremely poor" for the first 2 years of this 3 year study (Buchanan et al. 1990). Like red squirrels, Douglas squirrel populations are similarly limited by food supply (C. Smith 1968, 1970).

Management Effects

Vahle and Patton (1983) and Patton and Vahle (1986) recommended maintaining areas with closely spaced groups of trees of different ages and sizes. Stands of trees greater than 15 inches DBH are necessary to provide cone producing trees and nest trees. For Douglas-fir, 200- to 300-year-old trees are the best cone producers (Hermann and Lavender 1990). Additionally, one or more large tree components (>20 inches DBH), consisting of snags, fallen logs, and live trees, are necessary for primary middens. Closed canopies (basal areas ≥ 200 square feet per acre) are also important for maintaining mesic conditions for middens and suitable cover for nesting. To provide adequate conifer seed for food, 3 to 4 large (≥ 18 inches DBH) trees are needed per acre (Vahle 1978).

In mixed-species forests in canyons of the Southwest, other habitat components may exceed conifers in their importance for the red squirrel. Females in these areas typically produce 2 litters (versus 1 litter at higher elevations) per breeding season because of a greater abundance of summer

foods (fungi, berries, bird eggs) and superior nest sites (Uphoff 1990). Because these productive canyon areas are limited in number in the Southwest, they are particularly important squirrel habitat.

Habitat Management Recommendations

✓ Mixed-species and spruce-fir specialist

- Closed canopy VSS 4, VSS 5, and VSS 6

✓ Nesting

- Closed canopy VSS 4, VSS 5, and VSS 6 with interlocking crowns around nest sites
- Nests are close to middens
- Nest sites have high canopy cover and the best sites are mesic

✓ Foraging

- VSS 5 and VSS 6 (infrequent use of VSS 4)
- Middens have high canopy cover and are mesic, preserving cones
- High canopy cover provides mesic conditions for greater fungi production

✓ Other important habitat attributes

- Snags (>18 inches DBH) and downed logs (16-20 inches diameter) very important; smaller woody debris less important
- High canopy cover provides escape cover for squirrels
- Large mature cone-bearing trees, abundant fungi, and multistoried stands with many plant species in all forest layers constitute superior squirrel habitat
- Medium to large forest openings degrade the mesic microclimate in adjacent forests, and thereby reduce the quality of red squirrel habitat

Steller's Jay (*Cyanocitta stelleri*)

Steller's jays are a relatively large songbirds averaging 11.5 inches total length, weighing 0.25 pounds (Kilgore 1971). Steller's jays are a common resident of ponderosa pine and mixed-species forest, and occur often in goshawk diets. In eastern Oregon, 7.5% of goshawk prey remains were Steller's jays (Reynolds and Meslow 1984). Over 11% of the prey deliveries to 7 goshawk nests in north-central New Mexico were Steller's jays (Kennedy 1991). In northern Arizona, this corvid comprised 5.2% of 135 prey deliveries to 7 goshawk nests (Mannan and Boal 1990). Steller's jays were the most common prey in remains collected at a goshawk nest in piñon-juniper (K. Keel, A. Alexander and H. Reiser pers. obs.).

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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 $13.6 \pm 9.1\%$ 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%

Habitat Characteristics at Woodpecker Nest Locations and at Non-nest Random
Locations in the Elkhorn Mt, Helena National Forest Before (2002-2006) and After a
Mountain Pine Beetle Outbreak (2009-2011)

PROGRESS REPORT

October 2012

Submitted by

Vicki Saab, Jonathan Dudley, & Matt Dresser (Rocky Mountain Research Station &
Montana State University)

To

Denise Pengeroth (Helena National Forest)

Introduction

Recent epidemics of mountain pine beetles (*Dendroctonus ponderosae*; MPB) will fundamentally alter Rocky Mountain forests, impacting management decisions related to fire, logging, and wildlife habitat. We are studying effects of a recent MPB outbreak on nest-site selection and nest survival of 6 woodpecker species, and on occupancy dynamics of 46 avian landbird species in the Elkhorn Mountains, Helena National Forest. Here we report a summary of habitat characteristics measured at woodpecker nest locations before ($n = 89$; 2003-2006) and after the outbreak ($n = 124$; 2009-2011). We descriptively compare habitat characteristics at nest locations to non-nest random locations ($n = 76$), which characterize the average conditions on the landscape in our Elkhorns study area.

Methods

Habitat Measurements: To quantify the habitat changes associated with the MPB epidemic, we measured habitat characteristics at each of our 76 non-nest random point stations once before the beetle epidemic (in 2002-03) and again after the epidemic (2010). We measured the same vegetation characteristics annually at nest locations. Data were collected in 2012 at both random and nest locations but not included in this summary because the data entry is ongoing and incomplete as of October 2012. At each random and nest location, the vegetation plot was 2.5 ha in size and consisted of intersecting nested plots within 20m x 100m rectangles in a cross plot design (Saab et al. 2006; Figure 1). These vegetation plots were centered on focal trees at point count surveys (i.e. random locations) and nest trees at nest locations. Snags were defined as any standing dead (at least 50% of the needles dead or missing) tree ≥ 1.4 m in height measured in 2 size classes (small $\geq 3-9"$ [$\geq 8-23$ cm] and large $> 9"$ [>23 cm]) in diameter at breast height (dbh). Small snags and trees within 1 m, large snags within 10m, and large trees within 3m to either side of a 50m transect were tallied at each vegetation plot. These measurements were repeated in each cardinal direction. The total number of snags/trees counted per plot was then divided by the total area surveyed (e.g., $20 \times 50 \times 4 = 4000\text{m}^2$ per plot for large snags) to create the snag/tree density measurement. Species and dbh of the nest tree or focal tree at random locations was also recorded.

Nest Surveys: Nest surveys were conducted from 15 May - early July along belt transects (approximately 0.2 x ~0.8 km) (Dudley and Saab 2003). Transects were surveyed with the aid of playbacks, two times during the season. Birds that were detected during surveys were subsequently followed until their nests were found. A GPS location and notes describing the location were taken to allow for future visits. Once an occupied nest cavity was determined, nests were monitored every 3-4 days until fledging or failure.

Preliminary Results (see Table 1a)

Snag densities: Vegetation was measured annually at nest locations, and once before and once after the outbreak at random locations. Measurements were completed at 89 before (2002-2006) and 124 nest locations after (2009-2011) the outbreak, and at 76 non-nest random plots once before (2002-2003) and once after (2010) the outbreak. In 2010, large (> 9" dbh) live tree (all spp.) densities were reduced by nearly half (90.3 vs. 47.7 trees/ac), while large snag densities increased > 15 times (3.5 vs. 50.3 snags/ac) compared with pre-outbreak conditions at random locations. These changes are representative of average conditions on the landscape.

Pre-outbreak, all woodpecker species selected locations of higher large snag densities than those measured at random. Post-outbreak, however, snag densities at woodpecker nests were variable compared with random locations. Post-outbreak snag densities were significantly higher at three-toed woodpecker nests compared with random locations (73.3 ± 4.6 vs. 50.3 ± 3.1 snags/ac). Higher snag densities near their nests likely provided greater foraging opportunities for this beetle-foraging woodpecker.

Tree Species: Ponderosa pine (PIPO) is the dominant tree species (> 60% of tree composition) in our study units. Aspen (POTR) is rare on the landscape ($\leq 3\%$ of all tree species) but has been highly favored for nesting substrate, particularly pre-outbreak. Once conifer snags were recruited as a result of the outbreak, Hairy and three-toed woodpeckers shifted and expanded their nesting use of primarily aspen to ponderosa and lodgepole pines. Williamson's and Red-naped sapsuckers, downy woodpecker, and Northern flicker favored aspen as nesting substrate throughout the study.

Tree Diameter: Tree diameters were apparently not limiting to nesting woodpeckers in our study area. Average nest tree diameters were similar in size as those measured at random locations.

Discussion

Snag densities and diameters were similar between nest and random locations in the Elkhorn's study area except at nest locations of the Three-toed Woodpecker, a species selecting high densities of large snags. Three-toed woodpeckers specialize in foraging on bark beetle larvae and higher snag densities surrounding their nests likely provided greater foraging opportunities. This result suggests that high snag densities after beetle outbreaks are necessary for successful breeding of American three-toed woodpecker. Another notable result was the importance of aspen to nesting woodpeckers,

aspen woodlands to diversity - nesting birds and other
weed life has been well established (e.g., Neelon
& Saab 2011), and the Elkhorn study area is no
exception.



Temporal patterns of wolverine (*Gulo gulo luscus*) foraging in the boreal forest

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The foraging patterns and behaviors of predators can be discerned using GPS data. We used GPS data to investigate the temporal patterns of wolverine (*Gulo gulo luscus*) foraging on large prey in northern Alberta. We built a predictive model of wolverine large-prey events (beaver predation or ungulate scavenging) based on the spatial and temporal patterns of wolverine GPS data at foraging sites we visited in the field in winter. We used this model to predict large-prey events throughout our entire wolverine GPS dataset in winter and summer. We then evaluated how variables related to prey availability, seasonality, competition, and territoriality affected wolverine encounter time, residency time, and return time at predicted large-prey events. We found that wolverines encountered large prey more often in the spring when there is increased beaver and ungulate availability. The total time that wolverines spent at large-prey events was greater in winter (3.11 days [95th percentile = 2.62–3.63 days]) than summer (2.08 days [95th percentile = 1.70–2.51 days]), potentially because prey availability is limited in winter or prey is easier to capture in summer. Wolverines partitioned the total time at events into multiple visits, reducing their residency time and increasing their return time with each revisit, indicating biomass decline through time. The time between visits in winter (10.12 days [95th percentile = 7.99–12.56 days]) and summer (8.39 days [95th percentile = 7.18–9.74 days]) suggests wolverines might be patrolling their home range. We also found that wolverine residency time decreased and return time increased when there were other large-prey events available. Moreover, wolverine residency time at events increased when other wolverines were in the area. Our results suggest that large-prey events are important to the energy balance of wolverines and that wolverine foraging behavior is dynamic in response to environmental change.

Key words: Alberta, *Alces alces*, beaver, *Castor canadensis*, encounter time, *Gulo gulo luscus*, handling time, kill rate, moose, wolverine

The foraging patterns of predators can indicate the availability of prey on the landscape and the behaviors used to exploit them (Charnov 1976; Stephens and Krebs 1987). Predator foraging time can be divided into time spent finding and consuming prey. Researchers measure time spent finding prey as encounter time, or the time between encounters with prey items, whereas time spent consuming prey is measured as handling time, or the time from acquisition to consumption of prey. The time needed by predators to find prey is often dependent on the availability of prey (Holling 1959), whereas the time needed for consuming prey is frequently dependent on prey size (Knopff et al. 2010b; Cristescu et al. 2014). Researchers also have shown that there are a variety of other spatial and temporal variables, unique to the local environment, that have an effect on the time associated

with predators finding (Merrill et al. 2010; Whittington et al. 2011; McPhee et al. 2012) and consuming prey (Shrader et al. 2007; Courant and Fortin 2012; Stewart et al. 2017).

Direct observation is one way to measure encounter and handling times of prey (Stirling 1974; Klinka and Reimchen 2002). For example, observers can follow predators in the field to document the time between predation events (Miller et al. 2013). Although effective, tracking predators to estimate these parameters is time consuming and can be cost prohibitive. Researchers have recently developed statistical techniques that predict predation events from GPS data (Webb et al. 2008; Knopff et al. 2009; Ebinger et al. 2016). To create these models, one must have animal GPS data in tandem with a sample of predation events validated from field surveys. The information

Wolverine, *Gulo gulo luscus*, Resting Sites and Caching Behavior in the Boreal Forest

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Wright, Jonathan D., and Jessica Ernst. 2004. Wolverine, *Gulo gulo luscus*, resting sites and caching behavior in the boreal forest. Canadian Field-Naturalist 118(1): 61-64.

Wolverine (*Gulo gulo luscus*) caches and resting sites were examined in a study area in the boreal upland forests of northwestern Alberta and northeastern British Columbia (approximately 57°N). Cache sites were in climax, or "overmature" stands of Black Spruce (*Picea mariana*) or mixed-wood of high complexity, dominated by conifers, and in which the Trembling Aspen (*Populus tremuloides*) and Balsam Poplar (*Populus balsamifera*) component consisted of mostly dead or dying trees characteristic of such old growth in the boreal uplands. Sites offered relatively good visibility of the surrounding stand. Sites were never located in the dense to extremely dense homogenous spruce stands documented as being favored for travel by Wolverines in the study area. The better used cache complexes were accessed by numerous well-used trails made by the Wolverines themselves. Caches consisted of the bones, hide and hair of Moose (*Alces alces*) believed to have been killed by Grey Wolves (*Canis lupus*). Caches were classified as "simple caches" composed of a single feeding site and/or excavation and "cache complexes" involving one or more feeding "stations", latrines, resting sites, and climbing trees that may have been used as avenues of escape from competitors/predators. Resting sites were located atop the snow in relatively open locations that offered good visibility of the surroundings. Climax stands were implicated as being of importance to Wolverine caching behavior. Conservation implications include the detrimental effect on Wolverine populations likely to result from current timber harvesting practices in the boreal forest.

Key words: Wolverine, *Gulo gulo luscus*, cache, resting site, climax, boreal forest, stand, Alberta, British Columbia.

Knowledge gaps exist involving many aspects of Wolverine life history in forests, including caching behavior and selection of resting sites (Banci 1994). This paper presents observations of these aspects of Wolverine activities as documented over three winters (1997-2000) of snow-tracking efforts in the boreal upland forests of the border between northwestern Alberta and northeastern British Columbia, at approximately 57°N.

Methods

Wolverine and other furbearer activities were monitored during three winter seasons (1997-2000) utilizing snow-tracking methods. The tracking efforts covered approximately 1100 km² in the region of the border country of Alberta and British Columbia known as "Chinchaga" (after the Chinchaga River). Tracking is being increasingly recognized as a useful scientific tool in wildlife studies, management and conservation, with efforts being made to establish standardized terminology, to institute university courses on the subject, and to establish networks of trackers throughout the North American continent (Rezendes 1999; Zielinski and Kucera 1995). Snow tracking may be the only practical way of learning details of Wolverine habits and habitat use, as such details are not adequately provided by radio-telemetry studies (Eric Lofroth, personal communication).

Approximately 34 000 km were traveled by truck, snowmobile, cross-country skis and on foot, in search

of furbearer tracks over the course of the three winters, with an emphasis on locating Wolverines. Markedly different and readily divisible stand characteristics are a feature of the area as a result of the "Great Chinchaga Fire" which blanketed the region during the 1950s (Don Williams, personal communication), burning all but the upland ridges. Fifty years following the fire, two distinct forest types predominate: early-to-mid seral second growth of predominantly aspen or pine in the lowlands, with more limited late-seral, climax or "overmature" stands predominated by White Spruce and Black Spruce (*Picea* spp.), and mostly dead and dying *Populus* spp. in the uplands. The lowland forest may be further characterized as forming a mosaic broken by broad expanses of relatively open Black Spruce fen and open Willow (*Salix* spp.) muskeg. The upland forest cover is by comparison more continuous.

Moose (*Alces alces*) reach some of their highest densities in North America in the area (Brody 1981), being most heavily distributed in the lowlands, and frequent in the uplands. Groups of Woodland Caribou (*Rangifer tarandus caribou*) are frequent at low densities in the lowlands. These ungulates offer a generous prey base for the area's healthy Grey Wolf (*Canis lupus*) population, whose kills in turn offer a ready food source for the infrequent Wolverines.

When Wolverine tracks were located, the individuals were fore-tracked (older trails) or back-tracked (fresh trails) in order to gain insights into important and little-known details of the creatures' use of the