FOREST MANAGEMENT AND CONSERVATION OF BOREAL OWLS IN NORTH AMERICA

GREGORY D. HAYWARD

Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071 U.S.A.

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 reflecta la respuesta hipotesisada 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 from Canada to northern New Mexico (Palmer and Ryder 1984, Hayward et al. 1987, Whelton 1989, Stahlecker and Rawinski 1990). Throughout this broad distribution the owl occurs in a variety of boreal and subalpine forests: conifer and mixed forests in Canada (Bondrup-Nielsen 1978), transition forests in Minnesota (Lane 1988) and subalpine forests in the Rockies (Hayward et al. 1993). Boreal Owl populations are intimately linked to the composition, structure and dynamics of these forests (Hayward and Hayward 1993, Hayward and Verner 1994). Therefore, the distribution and abundance of Boreal Owls may be strongly influenced by forest management practices.

How do populations of Boreal Owls respond to alternative approaches in forest management? In this paper I provide a perspective on the potential impacts of forest management on the owl. Forest management represents the human activity most likely to influence the long-term distribution and abundance of Boreal Owls. Among Holarctic raptors, Boreal Owls, at least in the North American Rockies, may represent the species whose ecology is most universally tied to the forest system. An understanding of the potential response of Boreal Owls to various changes in forest structure and dynamics is a critical step in designing management.

In the U.S., management of Boreal Owls has become an important task on public lands. Four National Forest Regions and the Superior National Forest which represent most of the species' range south of Canada have designated the Boreal Owl as a "sensitive species." Within the National Forest System, sensitive species are plants and animals whose population viability is identified as a concern by a Regional Forester. Sensitive species require special management and programs are underway to develop management plans for Boreal Owls (J. Friedlander pers. comm.).

Unfortunately, the knowledge needed to develop a sound management strategy may be lacking (Hayward 1994a). To date, only four major published investigations from North America provide the ecological basis for management planning (Bondrup-Nielsen 1978, Palmer 1986, Hayward et al. 1992, Hayward et al. 1993). None of these investigations represent experimental approaches to ecological questions, none of these was designed to directly address forest management issues and all extended for 4 yr or less—a temporal scale insufficient to address important issues in forest management or the ecology of a long-lived verte-

brate. The Boreal Owl in North America represents a classic example of uncertainty in wildlife management.

Over 14 yr ago, Romesburg (1981) admonished wildlife managers for the development of management plans built upon unreliable knowledge. Management built on poor science leads to a loss of credibility and poor resource management. Current understanding of Boreal Owl ecology and biology is poor. Management built on this foundation alone will invite criticism and loss of credibility. Recently though, Murphy and Noon (1991) discussed an approach to deal with the inherent uncertainty associated with management of a forest raptor, the Spotted Owl (Strix occidentalis). They advocate applying the hypothetico-deductive approach to management. Through a rigorous assessment of the assumptions that form the basis of management, they reduce the uncertainty clouding an evaluation of the efficacy of various management options. Walters' (1986) adaptive management concepts are another attempt to deal with the uncertainty that accompanies wildlife management.

My perspectives on forest management for Boreal Owls is guided by a philosophy that combines the concepts of the hypothetico-deductive method and Walters' adaptive management to develop management in the face of poor knowledge. Therefore the statements I make regarding the potential response of Boreal Owls to forest management, must be regarded as hypotheses. I would advocate the testing of these hypotheses through multi-scale experiments in the spirit of adaptive management.

To provide a perspective on forest management and Boreal Owls, I will review the conservation status of Boreal Owls in North America including a discussion of trends in forest management, examine our understanding of the ecology of Boreal Owls as it relates to the owl's potential response to forest management, present some hypotheses concerning how different forest management approaches may influence Boreal Owls on different geographic and temporal scales and provide some ideas concerning strategies to approach forest management for Boreal Owls.

The perspective I present is biased by the geographic limits of my field experience with Boreal Owls—I have worked in the Rocky Mountains. More important, the literature on Boreal Owl ecology in North America is limited. Literature from Europe significantly broadens our understanding of the species. However, the ecology of Boreal Owls differs geographically within Europe (Korpimäki 1986) and within North America (Hayward et al. 1993). I suspect that the response of Boreal Owls to forest management differs between the Old and New Worlds and geographically within both.

Although our understanding of Boreal Owl ecology in North America is limited to three forest systems (one in each of northcentral Canada, central Idaho and northern Colorado), the Boreal Owl appears to occupy a variety of forest types. These forests range from deciduous and mixed forests to subalpine conifer forests (Meehan and Ritchie 1982, Palmer 1986, Lane 1988). The dynamics of these forests differ substantially due to differing patterns of forest growth and different disturbance regimes (Knight 1994). Likewise, Boreal Owl population dynamics, relationships with primary cavity nesters and relationships with prey populations differ among these forest types (Hayward 1994b). Therefore, the response of the owl to alternative forest management patterns almost certainly differs geographically. Any forest management scheme must be cognizant of the differences among the forest systems.

STATUS OF BOREAL OWLS IN NORTH AMERICA

Trends in population abundance or trends in habitat conditions are often used to assess status (Anderson 1991). In 1994, the U.S. Forest Service published an assessment of Boreal Owl status (Hayward and Verner 1994). That document concluded that Boreal Owls were not in immediate peril throughout their range but that over the long-term and in local areas over the short-term, Boreal Owls likely face significant conservation problems in the absence of conservation planning. To reach this conclusion the assessment examined evidence concerning trends in the distribution and abundance of the owl and the habitat relationships of the owl.

Distribution and Abundance of Boreal Owls. Little evidence exists to assess changes in the distribution of Boreal Owls in North America. Prior to 1979 the owl was not recognized as a breeding bird south of Canada (Eckert and Savaloja 1979). Since then numerous published reports have extended the recognized range of Boreal Owls in North America (Palmer and Ryder 1984, Hayward et al. 1987, Whelton 1989). Today, evidence exists for breeding populations throughout the Rocky Mountains south to southwestern Colorado and

northern New Mexico (Stahlecker and Rawinski 1990, Stahlecker and Duncan 1996). Do these records indicate an extension of the species range?

I suggest that the actual distribution of Boreal Owls has not changed recently, but our knowledge of distribution has increased because of an increase in survey effort. Historical records indicate that Boreal Owls were recorded in the western United States but not recognized as breeding. A closer look at the literature indicates that Boreal Owls were documented in Colorado for nearly 100 yr (Ryder et al. 1987). Despite the occurrence of Boreal Owls in the western U.S., checklists and field guides did not list the species even after breeding populations were documented in 1983. Biologists in Europe also located new populations of Boreal Owls during the past three decades and attributed these to increased interest in the species (Cramp 1977).

Direct evidence concerning trends in Boreal Owl abundance is completely lacking for North America. Breeding populations of Boreal Owls were only recently documented throughout most of the species' range in the U.S. Studies in North America generally have not focused on demography, precluding any assessments of trend in the near future. I am aware of only two populations (one in Idaho and one in Montana) that have been sampled using methods that will facilitate rigorous assessment of trends within the next 5 yr (Hayward et al. 1992). The prospects for assessing trends in the near future appear bleak.

Abundance and Distribution of Important Habitats. Information on trends in condition of forest habitats used by Boreal Owls offers an indirect method to infer population trends. Gathering and summarizing the necessary information at a broad geographic scale is not feasible for this paper. Furthermore, most statistics on timber harvest do not include the information necessary to evaluate the pattern in distribution and abundance of important forest types. For instance, stand-replacement harvests (clear-cuts) create stands without habitat value for Boreal Owls for a century or more, while partial cutting may leave stands with high habitat value if dominant trees are not removed. An objective evaluation of habitat trends relies not only on knowledge concerning recent timber harvest but knowledge on succession of lands that experienced large disturbance events 100-150 yr ago.

Maybe more important than the problems with describing impacts from past harvest are the difficulties in predicting future harvest. As the availability of timber has declined on lower elevation forest lands in western North America, focus is shifting to high elevation spruce-fir forests used by Boreal Owls. Furthermore, the rules regulating timber harvest in the U.S. have changed recently regarding salvage after fire (U.S. Public Law 104-19). The consequences of these changes are difficult to predict. As they might say in a prospectus, the extent of future harvest and therefore impact on Boreal Owl habitat may not be related to past trends.

Summary. There is little direct evidence concerning trends in North American Boreal Owl populations. In a Boreal Owl conservation assessment (Hayward 1994c), evaluation of habitat use patterns, life history and trends in habitat condition were used to infer owl trends.

HABITAT RELATIONSHIPS OF BOREAL OWLS

I review the habitat relationships of Boreal Owls. My goal is to establish the relationship between the owl and the forest to form hypotheses concerning the potential response of Boreal Owls to forest management.

Habitat relationships of Boreal Owls and habitat relationships of principal prey species will, in large part, dictate the potential response of Boreal Owls to timber management. The realized impact of forest management in a particular situation will be determined by the interaction of habitat relationships of the owl and prey populations mediated by those factors currently limiting population growth. Nesting habitat conditions (especially cavity availability), prey availability (winter and summer) and microclimatic conditions related to owl thermoregulation likely limit the distribution and abundance of Boreal Owls in different populations (Hayward 1994b). Management that focuses on these limiting factors, after examining evidence suggesting which factor may be most critical in a particular setting, will most effectively target management ac-

As I have emphasized, the ecology of Boreal Owls varies geographically. For instance, daily and annual movement patterns, relationship with principal prey populations, population stability and limiting factors vary from the boreal forests of Canada to southern New Mexico (Hayward et al. 1993). Despite this variation, Boreal Owls are forest owls throughout their range and their ecology is linked to forest habitats with particular structural

characteristics. I also consider nesting, roosting and foraging habitat separately because each of these may be limiting in different management settings. I will review the evidence describing the link between forest conditions and Boreal Owl populations. In my review I move from fine scale habitat characteristics to more broad scale relationships.

Fine Scale Habitat Relationships. Nesting habitat. The requirement for a large tree cavity constrains the range of sites used by Boreal Owl for nesting habitat. As secondary cavity nesters, boreals are intimately linked with the organisms and processes associated with formation of large tree cavities. An envirogram (Andrewartha and Birch 1984) emphasizes the linkage between forest structural conditions, primary cavity nester populations (woodpeckers), forest insects and pathogens (Fig. 1). The elements of the centrum relate directly to the owl while the web depicts components of the system important to maintaining the centrum. Elements of this envirogram are forest characteristics associated mainly with the presence/absence of suitable nesting cavities.

Beyond cavity availability, observations in the Rocky Mountains suggest that forest structural characteristics are important in nest-site selection. In Idaho, comparisons of forest structure at nest sites and random sites indicated use of stands with mature and older forest structure. Forest structure at nest sites differed from the random sample (101 sites) of available forest. Used sites occurred in more complex forest, with higher basal area, more large trees and less understory development than available sites (Hayward et al. 1993). Also in Idaho, a small nest-box experiment evaluated whether choice of nest sites is driven solely by cavity availability or if forest structure per se is important when a range of alternatives are available (Hayward et al. 1993). In this experiment nest boxes were hung in three forest types that differed significantly in structural characteristics. Owls used boxes in two forest types with complex structure (e.g., multiple canopy layers, many tree size classes) but did not use boxes in the forest type with a more simple structure (e.g., single canopy layer, more uniform tree diameters). Based on our observations I hypothesize that forest structure is important in an indirect way. Owls first search for nest sites in forests of a particular structure because the probability of finding cavities is highest in those types. So selection of old forest for nesting may be

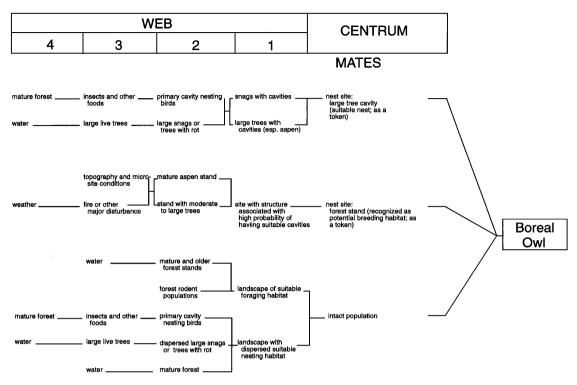


Figure 1. Envirogram (Andrewartha and Birch 1984) illustrating the relationship between Boreal Owls and specific components of the forest system. This portion of a larger envirogram (Hayward 1994b) focuses on Boreal Owl nesting ecology.

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 vear. 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 temperatures 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 Garton 1988, Hayward et al. 1993). Redbacked 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 access to small mammals during critical winter periods (Sonerud 1986, Sonerud et al. 1986). In Idaho, mortality and significant movement events most often occurred during warm winter periods when snow crusting became severe.

An envirogram further emphasizes the link between Boreal Owl foraging habitat and particular features of the forest, especially features linked with mature forests (see Hayward 1994b). The envirogram illustrates the indirect tie between Boreal Owl fitness and abundance of lichen, fungi and *Vaccinium* ground cover—all of which can be influenced by various forest management practices.

The evidence regarding habitat use for nesting, roosting and foraging in the Rockies suggests that at a fine scale, Boreal Owls rely on particular characteristics of mature and older forests. This relationship suggests that forest management at the level of stands will likely influence abundance of Boreal Owls.

Landscape Scale Habitat Relationships. Analysis of patterns of Boreal Owl abundance in relation to landscape patterns is not available for North America. Indirect evidence from Europe and North America suggests that Boreal Owls differentiate among forest habitats at the landscape scale. Our observations of owls in Idaho suggest that landscapes dominated by mature spruce-fir forest or those with mature spruce-fir juxtaposed with mature larch (Larix sp.), ponderosa pine (Pinus ponderosa) or aspen (Populus tremuloides) sites will have the greatest abundance of boreals (Hayward et al. 1992, 1993). In other words, an interspersion of forests that generally support high density of cavities in mature spruce-fir forest will provide quality habitat.

More direct evidence from Europe supports the notion that landscape scale forest cover influences Boreal Owl density and productivity. As the proportion of Scotch pine (*Pinus sylvestris*) forest decreased and the proportion of Norway spruce forest (*Picea abies*) and agricultural land increased, quality of territories (those with more frequent nesting) increased (Korpimäki 1988). The conclusion that territories with spruce forest and agricultural land (in small patches) were the highest quality habitat was corroborated by evidence on breeding frequency and clutch sizes.

Regional Scale Habitat Relationships. At very broad geographic scales, distribution patterns of Boreal Owls may also have important implications

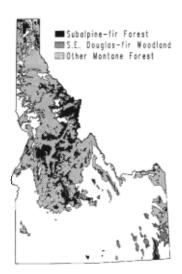


Figure 2. Pattern of potential Boreal Owl habitat in Idaho suggesting the distribution of a portion of the metapopulation extending along the Rocky Mountains. Potential habitat is defined as forested sites in the subalpine-fir zone throughout the state and Douglas-fir woodland in southeastern Idaho. Other montane forests are not considered potential habitat (adapted with permission of *Wildl. Monogr.* from Hayward et al. 1993).

for management. In portions of the boreal forest, distributions of Boreal Owls may be quite continuous. Along the southern and northern borders of the boreal forest and in the Rockies, the owl may occur in an interesting geographic pattern which likely results in a strong metapopulation structure (Hayward et al. 1993). In Idaho, patches of suitable habitat occur throughout the mountainous landscapes in a wide range of patch sizes (Fig. 2). Assuming that subpopulations of owls occupy habitat as hypothesized in Figure 2, the metapopulation structure of the owl in the region is a complex mix of subpopulations. Because of this structure, management of forest at the scale of individual national forests may have important implications for neighboring national forests over a broad geographic region.

HYPOTHESES: BOREAL OWL RESPONSE TO FOREST MANAGEMENT

Stand-Replacement Harvest. The importance of mature forest to Boreal Owls for nesting, roosting and foraging suggests that the short-term impact of stand-replacement harvest (clear-cut) will be negative. Open habitats as well as young, even-age forests provide few resources for Boreal Owls. Fur-

thermore, these habitats generally do not enhance habitat for woodpeckers or small mammals. Large clear-cuts appear to provide no resource values for Boreal Owls except along edges where owls may capture prey (Hayward 1994b). However, impacts will depend upon the size and spacing of cuts and the forest type being harvested. Furthermore, long-term impacts may not parallel short term response.

I hypothesize that small, patch clear-cuts implemented with long rotations may not negatively impact Boreal Owl habitat over the short- or longterm. Boreal Owls generally attack prey within 30 m of a perch (Hayward et al. 1993), so most of a 1-3 ha patch cut will be accessible for foraging. Furthermore, in small patch cuts, ground cover, which could reduce prey availability, often does not change significantly from that found under the forest, snow crusting affects only a small proportion of a small forest opening and small patch cuts emulate, to some extent, the landscape structure of mature spruce-fir forests (Knight 1994). In cases where small patch cutting is employed, I hypothesize that potential negative impacts will be reduced if the patch cutting is concentrated in a portion of each watershed rather than dispersed throughout entire watersheds and mature forest remains in the matrix between cuts.

Larger clear-cuts in conifer forest most often will reduce habitat quality for 100 to 200 yr. However, clear-cutting of aspen may be important in maintaining the long-term availability of cavities in some systems. In many forest systems aspen is a pioneer species that is lost through succession (DeByle and Winokur 1985). Restoration of aspen forests through silviculture may be an important management tool to maintain Boreal Owl habitat in forest systems where aspen provides a majority of the nesting habitat. Through coordinated timber harvest, large aspen which provide cavities for nesting may be maintained over the long-term, at the landscape scale, despite loss from individual stands. Focus on aspen management may even be more important in systems where aspen occupies a small proportion (<1%) of the landscape and occurs in small patches associated with particular microsites.

The shape of clear-cuts will likely influence both the short- and long-term impact on Boreal Owls. Although no direct evidence is available, I hypothesize that more complex shaped cutting units, especially those with stringers of forest extending into cutting units in upland areas, riparian buffers and patches of forest remaining within the cut unit, will have fewer negative impacts than large rectangular or circular cuts. This hypothesis stems from the pattern of habitat use by Boreal Owl prey species (Williams 1955, Merritt 1981, Wells-Gosling and Heaney 1984) and observations that Boreal Owls will nest in small patches of forest (G. Hayward unpubl. data).

Based on the same arguments, sloppy clear-cuts (clear-cuts with residual standing dead and live trees, especially aspen and patchy slash), and cuts that retain standing and downed wood on the site, will have fewer negative impacts, especially over the long-term. The mitigating qualities of retaining patches of live trees and shrubs, snags and woody debris arise from several factors. These elements will accelerate the rate at which the future stand attains mature and older forest characteristics (Knight 1994). In particular, recovery of fungi and lichen populations may be accelerated by maintenance of residuals (Ure and Maser 1982, Hansen et al. 1991).

Partial Cutting and Uneven-Age Management. Discussion of sloppy clear-cuts or irregular shelterwood prescriptions leads logically to discussion of partial cutting and uneven-age regeneration prescriptions. I hypothesize that group selection (harvest of small groups of trees in an uneven-age stand, maintaining the uneven-age properties) may not significantly reduce Boreal Owl habitat quality in many situations if, over the long-term, mature and old forest qualities are maintained and tree species composition does not exclude important cavity trees. Timber harvest prescriptions such as group selection and single tree selection (harvest of individual trees from an uneven-age stand in a pattern that maintains the size structure of the original stand) that retain forest structure, are compatible with developing owl nesting habitat. Thinning from below (harvest which removes individuals smaller than the dominant size class) and single tree selection that reduces competition among dominant trees and increases tree growth, could accelerate the process of developing suitable nest structures. While clear-cutting eliminates redbacked voles in Rocky Mountain forests (Campbell and Clark 1980, Scrivner and Smith 1984, Ramirez and Hornocker 1981), preliminary results of an experiment examining clear-cuts and group selection harvests indicate that red-backed voles remain abundant in partial cut stands when many large

trees are retained and ground disturbance is minimal (G. Hayward unpubl. data).

Broad Scale Predictions. Predicting the response of Boreal Owls to differing landscape scale patterns is more difficult. The lack of information on patterns of Boreal Owl abundance at the landscape and broader scales precludes extensive predictions at broad scales. I would argue that a primary focus of adaptive management approaches should be at this scale.

The issue of fragmentation seems to dominate much of the discussion of landscape scale impacts, so preliminary predictions regarding fragmentation may be useful in stimulating inquiry. In referring to potential response to fragmentation, I explicitly separate the influence of habitat loss from the influence of increased landscape heterogeneity. Fragmentation effects result from the process of changing the characteristics of the landscape mosaic and must be considered after eliminating the direct influence of reducing habitat area.

The high mobility and the extensive areas used on a daily basis by Boreal Owls suggests they may react to fragmentation differently from passerines. For instance, timber harvest of 30% of a basin through clear-cutting mature lodgepole pine (Pinus contorta) in 1-5 ha patches dispersed throughout the area may not significantly reduce habitat quality if the remaining forest is dominated by mature and older spruce-fir forest. The forests used by Boreal Owls exhibit a patchy mosaic under natural disturbance (Knight 1994). In a natural forest mosaic, owls move between distant patches on a daily basis (Hayward et al. 1993). This hypothesis assumes that timber harvest would not significantly reduce small mammal populations in the unharvested stands.

Aside from fragmentation, it is important to consider the impact of harvest schemes that target different forest types: aspen, lodgepole pine or old spruce-fir forests. I hypothesize that the negative impacts of any stand replacement harvest scheme will be decreased if stands of mature and older spruce-fir or aspen forest remain dispersed throughout the landscape.

Predicting the consequences of management at the broadest spatial scales is challenging. Conservation strategies at the regional scale should focus on maintaining the continuity of Boreal Owl metapopulations. This involves identifying subpopulations and landscapes that likely play key roles in the persistence of owls within the region and neighboring regions. These subpopulations would receive special attention to assure that management actions either favored the owl or did not negatively impact the subpopulation. Spatial modeling and good information on dispersal will be necessary to make sound management predictions at this scale.

STRATEGIES TO APPROACH FOREST MANAGEMENT FOR BOREAL OWLS

I began this discussion by emphasizing the extent of uncertainty in our understanding of Boreal Owls and noted the substantial geographic variation in Boreal Owl ecology across North America. In combination, these factors produce a discouraging management environment where predictions must be made tentatively. Therefore, the response of Boreal Owls to forest management was framed as a series of hypotheses to be tested and likely only testable through adaptive management. Despite the degree of uncertainty and the extent of geographic variation, I believe some general points can be made concerning approaches to forest management and planning for Boreal Owls.

Limiting Factors. Site-specific forest management for Boreal Owls must consider the factors most likely limiting the population in a particular setting. Thermal stress likely limits the elevation distribution of Boreal Owls in the central and southern Rocky Mountains. Therefore, availability of cool microsites, which often occur in mature and older forests, may be important in many regions.

The availability of nest cavities and prey likely limit populations of Boreal Owls in different situations. In regions with few or no Pileated Woodpecker (*Dryocopus pileatus*) or Northern Flicker (*Colaptes auratus*) cavities, nest-site availability will limit Boreal Owl abundance. Even within the geographic range of Pileated Woodpeckers, the absence of these woodpeckers at higher elevations may limit Boreal Owl abundance (Hayward et al. 1993). If cavity availability limits Boreal Owl populations, management of primary cavity excavators as well as the forest processes that support large snags will influence Boreal Owls.

In some forests, cavities are abundant and prey availability may play a strong role in Boreal Owl population dynamics. It is unclear whether absolute abundance or variation in prey populations is more important in owl population regulation. However, small mammal populations appear to be

linked to forest conditions (Hayward and Hayward 1995) and forest management will influence the abundance of potential prey, and in turn, affect owl population persistence. Forest structure will also influence the availability of prey by changing owl access to prey. For instance, forests with dense ground cover or a high density of small trees will reduce the efficiency of foraging Boreal Owls. Furthermore, forest structure affects snow conditions which influence prey availability (Sonerud 1986).

Cavity availability and prey availability likely interact to influence Boreal Owl population growth. Tree cavities occur nonrandomly across the landscape as do small mammal populations. The spatial arrangement of cavities and prey (relative to one another) are important in determining Boreal Owl abundance. The conservation status of Boreal Owls will be intimately tied to the interaction of these resources.

While cavities and prey likely limit Boreal Owl populations in most landscapes, predation and competition may influence populations in certain circumstances. In local situations, mustelids destroy a high proportion of owl nests in some years (Sonerud 1985). The influence of these losses on population abundance is unknown. Evidence also indicates that interactions with other owls may influence the distribution of Boreal Owls suggesting that competition may be an important limiting factor in some situations (Hakkarainen and Korpimäki 1996).

Boreal Owl Management Within Ecosystem Management. In western North America the ecology of Boreal Owls is linked with many characteristics of mature and older spruce-fir forests (Hayward 1994b). Management which facilitates the long-term maintenance of a landscape with significant representation of mature and older forest habitat will provide quality Boreal Owl habitat. Therefore, management schemes which promote the processes that maintain productive spruce-fir forests, and management which facilitates the stand dynamics necessary to produce old spruce-fir forest, will provide the habitat characteristics necessary for Boreal Owls. As indicated earlier, this is not incompatible with timber harvest.

Most applications of ecosystem management strive to manage systems to emulate natural disturbance patterns and processes. As reviewed by Knight (1994), spruce-fir forests experience a variety of disturbance agents that act at scales ranging from single trees to hundreds of hectares. Development of old forest conditions following stand replacement disturbance proceeds slowly; succession to mature forest conditions takes >150 yr. However, old forest stands represent a mosaic resulting from the frequent action of small scale disturbance. Partial cutting emulates (to some extent) insect mortality and windthrow, two common disturbances integral to the formation of old sprucefir forest structure. Alexander (1987:59) indicated that "uneven-aged cutting methods-individual tree and group selection—have seldom been used in spruce-fir forests, they appear to simulate the natural dynamics of these forests." Therefore, careful harvest of trees from spruce-fir forest may not be incompatible with maintaining important elements of old forest and habitat characteristics linked with Boreal Owls.

The paucity of information available on the response of Boreal Owls to specific forest management actions presents an obstacle to the formulation of management within an ecosystem framework. A strong conservation strategy for Boreal Owls cannot be produced without new knowledge on Boreal Owl ecology. Management based on current knowledge must contend with uncertainty and be devised specifically to deal with this uncertainty. Adaptive management (Walters 1986), then, must be built into any approach to manage the species, particularly an ecosystem management strategy.

Conclusions

Based on my review of the habitat relationships of Boreal Owls and management considerations, I offer the following conclusions: (1) Maintaining Boreal Owls on a local scale is not incompatible with timber harvest but is incompatible with extensive, stand replacement silviculture implemented over entire watersheds, employing large cutting units; (2) Forests with high habitat value for Boreal Owls develop through long successional trajectories. Therefore forest management must consider longterm forest patterns on broad spatial scales; (3) The hypothesized metapopulation structure of Boreal Owls in North America suggests that forest management must be coordinated at a regional scale; (4) Adaptive management which links managers and research ecologists is necessary to produce the knowledge needed to understand the response of Boreal Owls to alternative management approaches at a variety of spatial scales; (5) As a top carnivore that preys upon the dominant small mammal species in subalpine forests and nests in

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large tree cavities, the Boreal Owl integrates into its ecology many aspects of forest dynamics. As such, the owl may represent a good model to aid in developing ecosystem management; (6) At all spatial scales, an eye to restoration management must be taken in landscapes that have experienced intensive harvest in the past. Restoration may be particularly appropriate in aspen forests of the Rocky Mountains.

Forest management which sustains mature subalpine and boreal forests likely will conserve Boreal Owls. Such management, however, must consider (among other things) the successional dynamics of spruce-fir forests including the detritus food chain, the consequences of various disturbances and the long-term (post-glacial) trends in these forests. Management must focus as much on the long-term condition of the plant communities used by Boreal Owls as on the population dynamics of the owl.

ACKNOWLEDGMENTS

I sincerely thank Gerald Niemi and JoAnn Hanowski for organizing the symposium that led to the development of this paper. Erin O'Doherty, Edward (Oz) Garton, Ronald Ryder, Gerald Niemi and Daniel Varland reviewed an earlier draft of this paper; their comments were very helpful. The ideas presented here would not be possible without the dedicated fieldwork of many persons including folks who have aided in my field studies. Discussions with Pat Hayward, Floyd Gordon, Edward (Oz) Garton and Joan Friedlander have been influential in development of my philosophy of wildlife management in forest systems. Development of this paper was supported in part by U.S.F.S., Intermountain Forest and Range Experiment Station, RWU 4201.

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Received 2 November 1995; accepted 26 February 1997