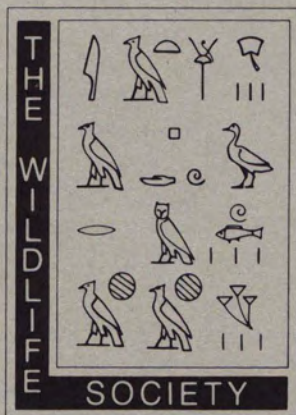


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# WILDLIFE MONOGRAPHS

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## **ECOLOGY OF BOREAL OWLS IN THE NORTHERN ROCKY MOUNTAINS, U.S.A.**

by

GREGORY D. HAYWARD, PATRICIA H. HAYWARD,  
AND EDWARD O. GARTON

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## WILDLIFE MONOGRAPHS

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Department of Fisheries and Wildlife Sciences,  
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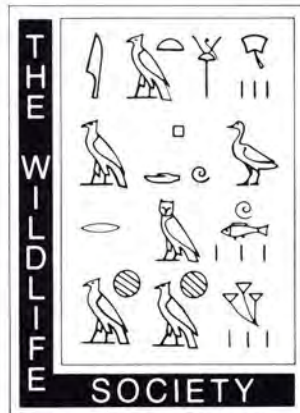
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FRONTISPIECE. Radio-marked male boreal owl (*Aegolius funereus*) in spruce-fir forest of central Idaho (photo by Patricia H. Hayward). The owl holds a recently captured southern red-backed vole (*Clethrionomys gapperi*), which was the most frequent prey species for both male and female owls.

# ECOLOGY OF BOREAL OWLS IN THE NORTHERN ROCKY MOUNTAINS, USA

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**Abstract:** We studied habitat use by boreal owls (*Aegolius funereus*) in the northern Rocky Mountains from January through August during 1984–88. Habitat use was examined at several spatial scales. The geographic distribution and range of life zones used by boreal owls were documented in western Montana, Idaho, and northwestern Wyoming. Habitat use, at the level of the home range, and microhabitats used for nesting, roosting, and foraging were observed in the Frank Church River of No Return Wilderness (RNRW) of central Idaho.

Boreal owls inhabited forests within the spruce–fir (*Picea* spp.–*Abies* spp.) life zone throughout the mountains of Montana, Idaho, and northern Wyoming. Nearly 90% of breeding territories located throughout this region were in subalpine fir (*Abies lasiocarpa*) habitat types (based on Steele et al. 1981), and no owls were detected below 1,292 m. Within the RNRW, owl breeding sites occurred ( $n = 28$ ) in mixed-conifer (39%), spruce–fir (25%), Douglas-fir (*Pseudotsuga menziesii*) (18%), and aspen (*Populus tremuloides*) (18%) stands. Lodgepole-pine (*Pinus contorta*) forest, which was the most common vegetation type in the area, was not used for nesting. Nest sites were restricted to mature and old forest stands with complex physical structure. Roosting habitat differed between winter and summer. Winter roosts differed little from available forest cover whereas summer roosts had greater canopy cover, higher tree density, and higher basal area than paired random sites. During summer, the owls used cool microsites for roosting; during hot weather, boreal owls frequently exhibited symptoms of heat stress by gular fluttering and perching with wings lowered. The best foraging habitat was associated with older spruce–fir stands. These sites had prey populations 2–10 times greater than other sites and provided open forest structure that facilitated hunting. Because of the wide geographic dispersion of suitable nesting, roosting, and foraging habitat, the owls used large home ranges; ranges averaged  $1,451 \pm 552$  ha in winter ( $n = 13$ ) and  $1,182 \pm 335$  ha in summer ( $n = 15$ ).

Boreal owls at our intensive study site fed primarily on small mammals in both winter and summer. During both seasons, southern red-backed voles (*Clethrionomys gapperi*) were the most frequent prey, composing 36% of all prey items. In winter, northern flying squirrels (*Glaucomys sabrinus*) were captured by females (14% of prey items) but not males. During snow-free seasons, boreal owls captured northern pocket gophers (*Thomomys talpoides*), yellow-pine chipmunks (*Tamias amoenus*), and western jumping mice (*Zapus princeps*) that were unavailable when the ground was snow covered.

The size of breeding populations and breeding success varied from year to year. During 1 of 4 years, few owls attempted to breed, and we knew of none that raised young. Estimates of demographic characteristics of boreal owls suggest that the population declined during our investigation. We estimated annual adult survival as 46% (95% CI = 23–91%), and production by nesting females averaged 2.3 ( $\pm 0.542$ ) young per successful nest. We documented long distance movements by adult owls, which support the contention that immigration of nomadic owls may help maintain populations that would otherwise face local extinction.

These results suggest that conservation of boreal owls will require forest management that maintains the distribution and abundance of mature and older forest stands. Because boreal owls in the northern Rocky Mountains occur in a narrow life zone, populations exist in isolated patches that cover a relatively small portion of the landscape. To maintain quality habitat at any given site will require snag retention and timber harvest practices that retain forest structure. A shift to uneven-age management or modifications of even-age systems that retain particular old forest characteristics in spruce–fir forest should meet the owls' needs for nesting structures and roosting sites while maintaining prey populations.

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## INTRODUCTION

Boreal owls (*Aegolius funereus*), referred to as Tengmalm's owl outside North America, occur throughout the holarctic in boreal climatic zones. On each continent, disjunct populations occur in mountains south of the broad transcontinental boreal forest populations, which extend from Scandinavia eastward across Asia and from Alaska through Canada to the Atlantic (Cramp 1977, Voous 1988). Boreal owls located in mountain regions of Europe and Asia have long been recognized as isolated

resident breeding populations, whereas in North America, breeding status was only recently documented in the mountains of the western United States (Hayward and Garton 1983, Palmer and Ryder 1984, Hayward et al. 1987a, Whelton 1989). Studies of this species, mainly in Scandinavia, Germany, and France, indicate that the biology and ecology of boreal owls varies geographically and is strongly related to local forest conditions and prey populations.

Boreal owls inhabit forested habitats where they nest exclusively in tree cavities



or artificial nest structures (Mikkola 1983). Nesting habitat includes a range of vegetation types depending on geographic region. In Scandinavia, studies report nests in artificial structures hung in pine (*Pinus* spp.), spruce (*Picea* spp.), and birch (*Betula* spp.) forest (Norberg 1964, Korpimäki 1981, Solheim 1983a). In France, "mountain pine" (*Pinus uncinata* and *P. sylvestris*) forest and old forest stands with beech (*Fagus* spp.) trees were used by owls located by DeJaifve et al. (1990:267) and Joneniaux and Durand (1987), respectively. In Germany, conifer forest with old trees was used for nesting (Konig 1969, Jorlitschka 1988). Nest sites in Canada and Colorado have occurred mainly in spruce, aspen (*Populus tremuloides*), and mixed forests (Bondrup-Nielsen 1978, Palmer 1986). Although foraging habitat has not been studied extensively, observations in Scandinavia suggest that old spruce forest is important, especially during winter. Clearcuts and cultivated fields are used for hunting only in early spring before vegetation becomes dense (Sonerud 1986, Korpimäki 1988a).

Small mammals, particularly voles (*Clethrionomys* spp. and *Microtus* spp.), are primary prey of boreal owls throughout their geographic range. Voles frequently account for over 75% of prey items identified in pellets and prey remains at nests (Klaus et al. 1975, Korpimäki 1981). Other prey include shrews, mice, birds, and insects (Cramp 1977). The range of prey consumed increases in southern regions of Europe where the owls are considered generalist predators (Solheim 1983a; Lofgren et al. 1986; Korpimäki 1986, 1987a). In northern regions with pronounced vole cycles, boreal owls function as microtine specialists and exhibit extreme fluctuations in breeding parameters (Korpimäki 1986). Breeding population size, laying date, clutch size, fledging success, and the frequency of bigyny and biandry all vary among years and geographically, corresponding to variation in prey availability (Carlsson et al. 1987, Korpimäki 1987b). Local breeding densities during good prey years exceed 4 pairs/

km<sup>2</sup> whereas in poor years few owls initiate nesting (Lofgren et al. 1986, Schelper 1989). These studies demonstrate how geographic variation in prey populations influence local boreal owl populations.

The influence of prey populations on boreal owl ecology extends from population dynamics, mating system, and habitat use to yearly movement patterns (Mysterud 1970, Lundberg 1979, Lofgren et al. 1986). Korpimäki (1986) hypothesized that conflicting selective pressures of nest site scarcity favoring site tenacity and fluctuating prey availability favoring nomadism have resulted in a variety of movement patterns in boreal owl populations. Where boreal owls consume a varied diet and prey availability fluctuates little, populations are resident. Under conditions of reduced prey diversity and moderate prey fluctuations, populations exhibit a strategy of partial migration (males are resident and females nomadic) whereas in areas with pronounced vole cycles, adults are nomadic (Korpimäki 1986, Lofgren et al. 1986). Migratory status in North America has not been systematically investigated. In eastern and central North America, irruptions are evident (Catling 1972, Evans and Rosenfield 1977) but the phenomenon has not been noted in the West.

Based on the variety of ecological patterns described for boreal owls in Europe, it is difficult to predict the ecological characteristics of populations in western North America. The relationship among boreal owls, forest habitat, and small mammal populations, however, suggests that understanding patterns of habitat use and prey relationships will be central to the formulation of conservation programs and to understanding the owl's ecology (Scott et al. 1987).

In this study, we investigated habitat use by boreal owls in the northern Rocky Mountains of the United States. We approached the study of habitat from a broad perspective by investigating natural history and by examining habitat use on several scales (i.e., several levels of resolution from a regional to microhabitat scale). Prior to our investigation, information on bo-

real owl habitat use in North America was limited to a study in Canada (Bondrup-Nielsen 1978) and a concurrent investigation in Colorado (Palmer 1986). Established breeding populations of boreal owls had been observed in central Idaho and Colorado (Hayward and Garton 1983, Palmer and Ryder 1984); otherwise, the extent of the species' distribution south of Canada was completely unknown.

Our goal was to describe habitat use by boreal owls at several scales emphasizing regional distribution and microhabitat use. We also sought to describe population characteristics (e.g., population trend, productivity), both to place the habitat data in an ecological context and to assess the species' current status. To meet these goals we pursued 5 specific objectives: (1) to estimate the geographic extent of boreal owl populations in the northern Rocky Mountains within the United States, (2) to estimate breeding habitat associations and life zone of boreal owls in this region, (3) to describe habitat use for nesting, roosting, and foraging in 1 local population of boreal owls, (4) to estimate seasonal and yearly movement patterns of boreal owls in 1 local population, and (5) to describe demographic characteristics of boreal owls in 1 local population.

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## STUDY AREA

To examine habitat use at multiple geographic scales, we examined broad patterns through extensive field studies at a regional scale (covering several states in the northern Rocky Mountains) and examined fine scale patterns on a local scale (including 2 study areas, each encompassing over 6,500 ha, in the wilderness of central Idaho). We allocated our effort disproportionately, emphasizing field work at the intensive study site.

Our broad scale surveys for boreal owls included portions of the northern Rocky Mountains from northern Idaho and Montana to northern Wyoming and Utah. Co-operators throughout this region surveyed for owls on 13 national forests, including the Idaho Panhandle, Kootenai, Flathead, Lolo, Lewis and Clark, Beaverhead, Nez Perce, Payette, Salmon, Boise, Caribou, Bridger-Teton, and Fishlake national forests. Owl surveys were restricted to coniferous forest but extended from lower conifer tree line (Ponderosa pine, *Pinus ponderosa*, forests) to upper timberline. Our investigation in this broad geographic region was limited to areas that had roads providing winter access to the higher elevation forests.

Our intensive investigation was in the mountains of central Idaho in the northern portion of the 956,515-ha Frank Church River of No Return Wilderness (RNRW) (Fig. 1). The study area extended from 1,580 to 2,400 m elevation in a high, dissected plateau surrounded on 3 sides by deep, rocky canyons that plunge to 700 m elevation along the Salmon River. The entire area is mountainous but lacks steep jagged peaks; few slopes exceed 50%.

Climate in the RNRW has a strong Pacific coastal influence during winter but follows continental patterns in summer (Finklin 1988). At 1,700 m elevation, Chamberlain Basin Guard Station receives 76 cm of precipitation per year (50% as snowfall). Snow depths reach 50–90 cm at

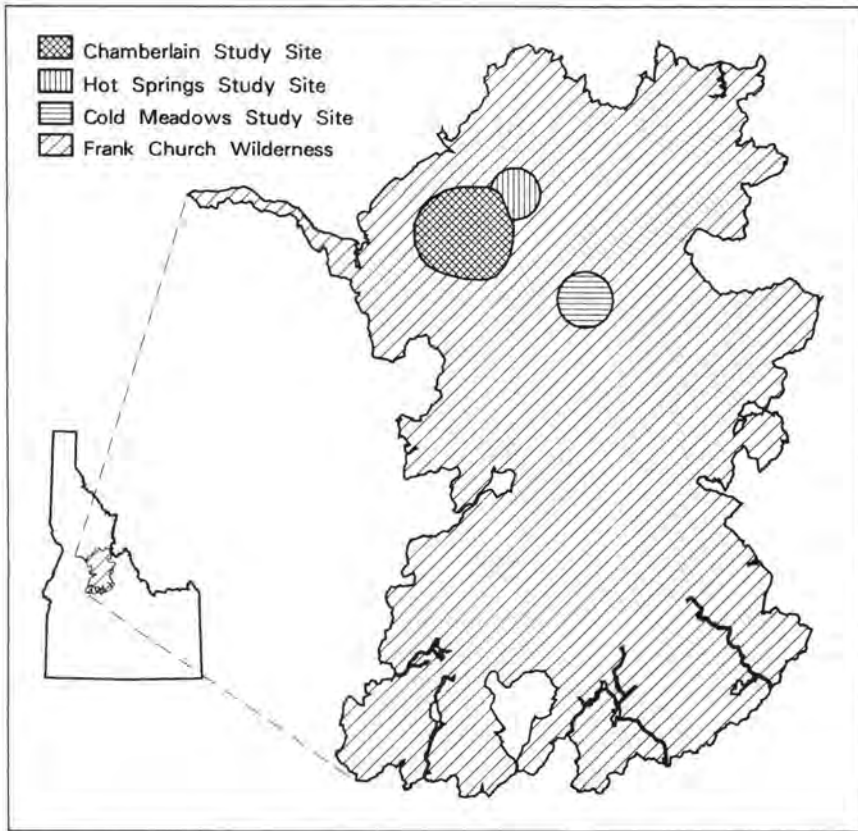


Fig. 1. Location of Chamberlain, Cold Meadows, and Hot Springs Meadow study sites in the 956,500-ha, Frank Church River of No Return Wilderness in central Idaho.

this elevation. At 2,150 m, 70% of precipitation is snowfall, and snow depths exceed 150 cm. The frost-free period at 1,700 m lasts 35–40 days. In July, maximum temperatures averaged 28 C with average minimums of 5 C; in February, daily temperature extremes averaged 5 C maximum and –20 C minimum at 1,700 m.

We established 3 study sites in the northern mountains of the RNRW—hereafter referred to as Chamberlain, Cold Meadows, and Hot Springs Meadow (Fig. 1). The Chamberlain site, where 90% of our field effort was centered, included a 35,000-ha portion of Chamberlain Basin, particularly the basin upstream from the junction of the West Fork and Chamberlain Creek. Cold Meadows included about 9,000 ha within 5.5 km of Cold Meadows Guard Station. This site is 30 km east of Cham-

berlain Basin Guard Station at 2,130 m elevation and provided access to lodgepole-pine (*Pinus contorta*) and spruce-fir forests. Hot Springs Meadow site, 8 km northeast of Chamberlain Basin Guard Station, included about 6,000 ha surrounding the Hot Springs Meadow cabin at 2,160 m and also provided access to spruce-fir forest.

The landscape of all 3 study sites within the wilderness study area was dominated by coniferous forest (Fig. 2). Prior to the initiation of the study, most forest stands in the area exceeded 125 years old except for a 2,225-ha area that burned in 1966. Lodgepole pine dominated the forest, especially in cold-air drainages where monospecific stands of this species covered areas exceeding 300 ha. Southern slopes below 1,825 m supported open forest of 60–130-



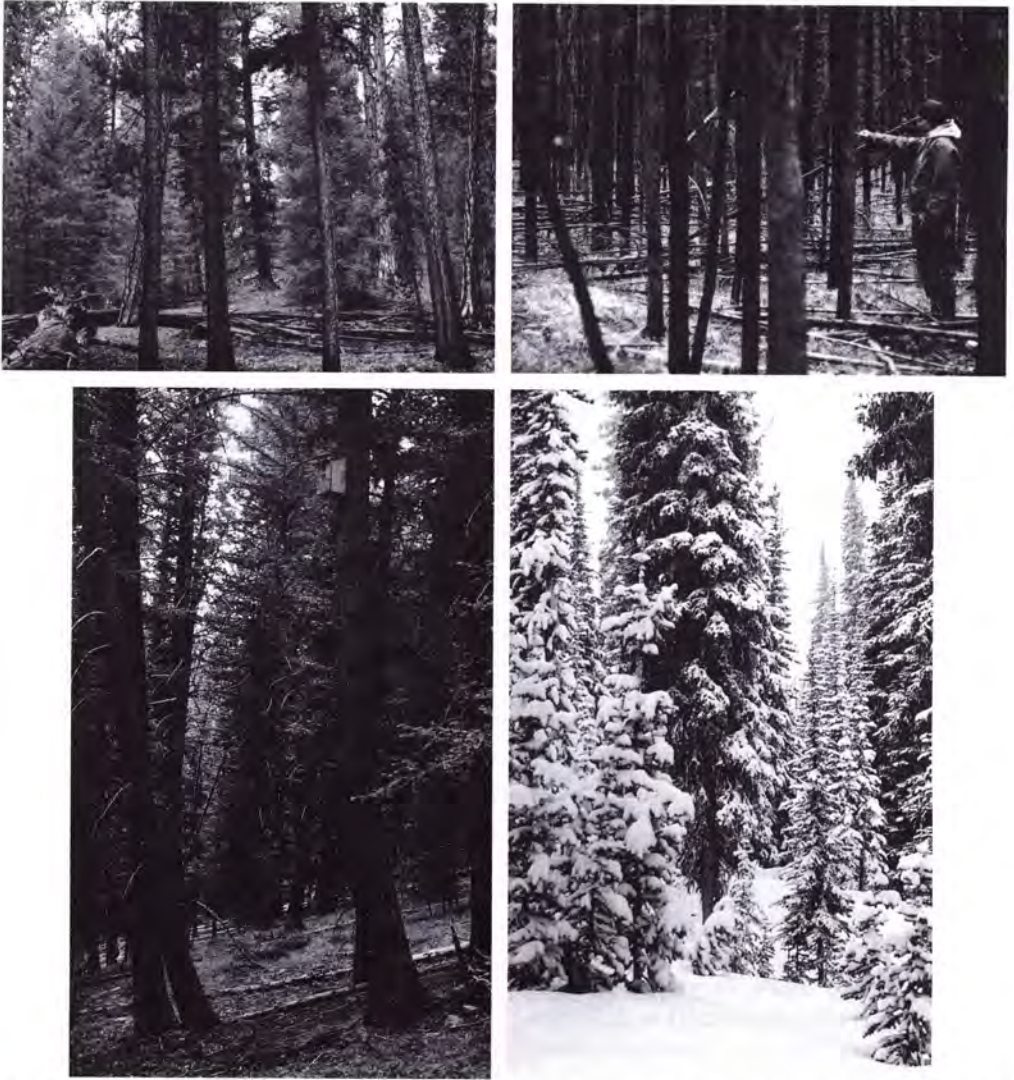


Fig. 2. Contrasting structure of 4 major conifer vegetation types that dominate the landscape of the Frank Church River of No Return Wilderness study sites. Stands shown here include (upper left) old mixed-conifer forest dominated by ponderosa pine on southeast exposure of Flossie Creek drainage; (lower left) old Douglas-fir forest on northeast exposure of Hotzel Creek drainage; (upper right) mature lodgepole-pine forest in frost pocket along Chamberlain Creek; and (lower right) mature spruce-fir forest on west exposure near top of Trout Creek drainage.

cm Ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*). These forests are called mixed conifer throughout this text. On cooler aspects up to 2,000 m, Douglas-fir dominated unless recent fire had produced a lodgepole-pine forest. Douglas-fir forests were mixed with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) up to 2,200 m. Above 2,000 m, spruce-fir forest occupied sites without recent fire.

Meadows and open shrub fields covered <3% of the area. Sagebrush-bunchgrass (*Artemisia* spp.-*Festuca idahoensis*) slopes were the most common open habitat below 1,850 m whereas *Carex* meadows and willow (*Salix* spp.) bogs occurred at higher elevations. Aspen occurred in small clumps (usually <0.5 ha) below 2,100 m and covered <1% of the landscape.

For the Chamberlain study site, we classified the landscape by dominant overstory

vegetation using color 1:5800 aerial photographs. Rank order of landscape coverage from most to least dominant were lodgepole pine, Douglas-fir, mixed conifer, spruce-fir, meadow and shrub-field openings, and aspen. Lodgepole-pine forest covered over 50% of the Chamberlain site.

Other species of owls that were heard calling each year in the RNRW included northern pygmy owl (*Glaucidium gnoma*), northern saw-whet owl (*Aegolius acadicus*), great horned owl (*Bubo virginianus*), and great gray owl (*Strix nebulosa*). Barred owls (*S. varia*) called each year after 1984. Long-eared owls (*Asio otus*) were seen occasionally but may not nest in the area, whereas flammulated owls (*Otus flammeolus*) were heard during 3 years in the mixed-conifer stands. Two important primary excavators, pileated woodpecker (*Dryocopus pileatus*) and northern flicker (*Colaptes auratus*), breed in the area but are most abundant in the lower elevations.

## DEFINITIONS

Several terms used loosely in the ecological literature are defined below to clarify our use of the terms:

1. A forest stand is a homogeneous portion of forest that can be differentiated from surrounding units by age, composition, structure, or geography (Daniel *et al.* 1979).
2. Microhabitat refers to conditions within an area smaller than a forest stand—a site where an individual owl performs a single activity such as roosting, nesting, or foraging.
3. Macrohabitat refers to characteristics of the environment in an area large enough to include an individual's seasonal home range. For boreal owls, forest stands are convenient elements to measure for macrohabitat description because home ranges are composed of numerous forest stands. Macrohabitat, then, generally includes several vegetation types and land forms and is quantified by the proportion of area covered by each.

We believed that existing definitions of

forest age and structure, especially definitions of old growth, were not adequate for the forests of central Idaho (Hayward 1991). Here we apply the following working definitions of stand age (*see* Hayward 1991 for more details):

1. Young forest—forest with few or no seed-producing trees, where seedling establishment is common and leaf area is increasing. Structurally, a young forest stand is dominated by small trees that are growing vigorously.
2. Aggradation stage forest—a forest stand in which tree establishment is significantly reduced and competition has resulted in tree mortality, but stand structure is primarily a result of the major disturbance that created the stand. Aggradation stage forest, then, has trees of a single age class, new snags, and few seedlings.
3. Mature forest—a stand that has developed long enough since catastrophic disturbance that mortality and regeneration are prominent processes and regeneration results from parent trees in the stand. The mature stand has tree-fall gaps created after stand establishment and an uneven-age tree diameter distribution.
4. Old forest—a stand whose age and physical structure is currently influenced by processes within the stand rather than the last catastrophic disturbance. Old forest will have a wide variety of tree sizes and ages and a patchy structure resulting from tree mortality and regeneration.

## FIELD METHODS

We conducted field work from 26 January to 28 September 1984, 26 January to 28 August 1985, 14 January to 12 October 1986, 16 February to 23 August 1987 and for 2 weeks in both February and May 1988.

### Locating and Capturing Owls

*Extensive Surveys in the Northern Rockies.*—We estimated the regional dis-



tribution of boreal owls from winter surveys conducted in the northern Rockies (the Rocky Mountains south of Canada and north of 42°N). We divided the region included in these surveys into 2 groups based on differences in climate that result in different forest structures. The northern group included the Flathead, Idaho Panhandle, and Lolo national forests. This region experiences abundant rain and snowfall and moderate temperatures from maritime air masses (Arno 1979). Stands on the Beaverhead, Salmon, Caribou, and Payette national forests experience a continental climate with cooler winter temperatures and less summer moisture. These more southern forests support smaller trees and a less developed shrub layer.

During February–April 1984–86, personnel from 13 national forests, Grand Teton National Park, Wyoming Game and Fish, and the Garnett District of the Bureau of Land Management searched for boreal owls by foot, car, and snowmobile using playback of tape-recorded boreal owl staccato song (Bondrup-Nielsen 1978). Biologists were recruited for the survey with the understanding that our objective was to estimate the geographic extent and elevation range of the species in the northern Rockies. Therefore, biologists were not instructed to concentrate surveys in certain habitats or particular geographic locations. Surveys were conducted from 500 to 3,050 m elevation with over 80% being over 1,280 m. No explicit effort was made to repeat survey routes during any year; however, biologists did resurvey some areas.

Playback surveys began in evening when darkness permitted viewing the first stars. Biologists traveled forest roads stopping every 1–2 km, depending on terrain, to call for owls. At each calling stop, the biologist played 3 series of owl calls of 2-minute duration and listened for a response for 2 minutes after each series. Playback tapes for the geographic survey were compiled by G. D. Hayward using 3 source recordings, and duplicates were distributed to 60 cooperators. The master recording included boreal owl songs recorded in Alberta, Canada, a recording from

Cornell Laboratory of Sound, and a recording from the Soviet Union supplied by R. A. Ryder (Colo. State Univ.). These 3 recordings were segregated on the tape into 3 segments approximately 6 minutes long. Songs recorded from 1 of these geographic localities were broadcast at each playback station. Cooperators were advised to conduct surveys during good listening conditions (low wind, no rain, no heavy snowfall).

*Locating Potential Nest Sites in the RNRW.*—We used similar playback surveys to estimate the elevational distribution of boreal owls and to locate individual breeding sites in the RNRW. All wilderness surveys were conducted on skis from January through April in 1984–87. Beginning when the first stars became visible, we played tape recordings of the boreal owl staccato song at 0.5–1-km intervals along trails and ridge lines. We remained at each calling station 10–12 minutes playing 3 series of staccato song with 2 minutes of silence after each series. In addition to time spent listening for owls at each calling station, we paused for 1 minute at least once between stations. We sampled available habitat along survey routes radiating 10 km from field lodgings at Chamberlain and about 5 km from Cold Meadows and Hot Springs Meadow. Some survey routes followed existing trails radiating from each study site whereas others followed ridge lines and stream courses. Routes at Chamberlain and Cold Meadows were laid out to access at least 80% of the landscape within 5 km of the camp. At Chamberlain, routes extended up to 10 km from the camp, but coverage of the landscape in the outer 5-km “donut” was less complete. Because Hot Springs Meadow was surveyed less intensively and in only 1 year, coverage was limited to about 50% of the area within 5 km of the camp.

At Chamberlain and Cold Meadows, each route was surveyed 2–5 times a year. When we heard owls during a survey, we skied toward the singing male in an attempt to locate the potential nest site. Locations were not considered potential breeding sites for habitat analysis unless



they met 1 of 3 criteria: (1) we located an active nest, (2) we heard both a male and female boreal owl courting at the site (Bondrup-Nielsen 1978), or (3) a male was heard singing at the site more than once during a year.

*Capture and Radio Tagging.*—We captured and radio tagged boreal owls at the Chamberlain site to study movements, habitat use, food habits, and survival. We trapped owls during January–May at potential breeding sites located during playback surveys. After locating a site with a singing-male boreal owl, we returned to the site 1–15 nights later and set 10 bal-chatri traps and a mist net within 100 m of the singing location (Bull 1987). We hung the mist net in an aisle in the forest along the contour. Bal-chatri traps baited with a live vole (*Microtus* spp.) or deer mouse (*Peromyscus maniculatus*) were placed 5–60 m from the mist net. Beginning at dark, a recorded staccato song was played for 20 minutes each hour from beneath a tree about 3 m from the net. Captured owls were retrieved immediately from the net and traps were checked each hour. This method was effective for capturing both male and female boreal owls.

Captured owls were weighed and measured to determine sex (Hayward and Hayward 1991), and, beginning in 1986, wing-molt pattern was recorded to determine age (R. Solheim, Zool. Inst., Oslo, Norway, pers. commun.). We radio marked the owls with 6-g, backpack-mounted radio transmitters (Wildlife Materials, Inc., Carbondale, Ill., model MPB-1220-LD) with an expected battery life of 150 days (Hayward 1987). The backpack harness that held the transmitter on the owl's back was made of 4-mm-wide elastic webbing. The elastic webbing was sewn together with upholstery thread to assure permanent attachment. Each harness was individually fitted so that the tip of a person's little finger could slip between the owl's back and the transmitter.

Radio-marked owls were recaptured and outfitted with a new transmitter after approximately 140 days or when abnormalities in the radio signal indicated potential

transmitter failure. We recaptured owls from their daytime roosts with a dip net on a 5.5-m fiberglass-extension pole or a miniature mist net (2.5 m long and 1.5 m tall) as we described in Bull (1987).

### Microhabitat Measurements

*Breeding Habitat.*—We characterized the structure of forest stands at confirmed nest sites and potential breeding sites (male-singing locations) by measuring forest vegetation, topographic features, and habitat type on a plot within the nest or singing stand. We considered singing sites that met the criteria defined above for potential breeding sites as representative breeding habitat. Our observations of radio-marked owls and observations by Bondrup-Nielsen (1978) and Palmer (1986) all indicate that boreal owls do not sing from sites throughout their home range. Rather, they consistently sing within 100 m of a potential nest cavity.

Forest structure was measured in a 30-by-125-m plot centered on the nest or singing location but within a single forest stand—the plot was not bisected by any abrupt ecotone. In cases where a nest or calling site lay near an ecotone, we placed the plot in the stand in which the nest or calling tree was rooted. If we had measured a combination of both forest stands at an ecotone, the resulting vegetation description would not have typified either forest stand, but rather some average stand that did not exist (Mueller-Dombois and Ellenberg 1974). Within the forest stand, structure was quantified by density of trees and by percent cover of trees, shrubs, grasses, and forbs.

Cover of trees and shrubs was sampled along 8 30.5-m-parallel transects placed perpendicular to the slope within the plot (Bonham 1989). Transects were randomly spaced 6–30 m apart. Intercept measurements along these transects provided shrub cover estimates (all shrubs were <1 m high) and tree cover estimates in 5 height categories (canopy cover layers) (0–1 m, 1.1–2 m, 2.1–4 m, 4.1–8 m, >8 m) (Bauer 1943, Borman and Buell 1964, Hayward and

Garton 1988). We recorded the dominant tree species and number of trees and snags in 6 diameter-at-breast-height (dbh) classes (2.5–7.6 cm, 7.7–15 cm, 15.1–23 cm, 23.1–38 cm, 38.1–53 cm, and >53 cm) within 16 systematically located 83-m<sup>2</sup>-circular plots, 2 per transect (modified from James 1971, Hayward and Garton 1988). Cover of forbs, grasses, and subshrubs (any woody plant species commonly under 15 cm tall) was estimated on 16 0.1-m<sup>2</sup>-rectangular quadrats (Daubenmire 1959), 2 quadrats per transect.

Because the small (83-m<sup>2</sup>), circular tree plots would underestimate numbers of large diameter trees, variable-radius-plot tree samples were measured from 4 points—1 point along each of transects 2, 4, 6, and 8. We used a relaskop (Spiegel, Inc., Germany) with a 10-factor prism and 30-cm-dbh lower limit to count trees. Densities and basal area were calculated as described by Avery (1975:170).

In addition to measuring forest structure, we recorded topographic variables (aspect, slope, topographic position, and distance to water) and classified the forest vegetation within the nest stand or potential breeding site by habitat type (to the level of phase) (Steele et al. 1981). "Habitat type" as used by Steele et al. (1981) refers to a particular method of vegetation classification based on potential forest vegetation and environmental conditions. Habitat type differs from vegetation type in that vegetation type is defined by vegetation currently on a site and habitat type is determined by vegetation potential. Throughout this text "habitat type" will refer to forests classified using this method.

We measured forest structure using these procedures at owl locations in the RNRW and sites located throughout the northern Rockies. For sites outside the RNRW, however, we used only 4 transects and measured all variables with half as many subsamples.

*Available Breeding Habitats.*—Four cover types (lodgepole pine, spruce-fir, mixed conifer, and Douglas-fir) together represented over 99% of the forest cover in the study area. We chose 25 random

points in each of the 4 types from throughout the study area (26 in mixed conifer by accident) using a random-number table and map-grid overlay. Random sites were classified into 1 of the 4 types based on overstory species composition. At each site we measured forest structure to define the physiognomy of the stand. Methods followed those described above for breeding habitat except that we used only 4 line-intercept transects and all variables were measured with half as many subsamples.

We chose to select a stratified random sample because a strictly random sample would have been dominated by lodgepole-pine forest, a vegetation type in which the owls did not nest. Instead we sought to obtain a sample that would adequately describe the full range of forest physiognomy of each cover type occupying 5% or more of the study area. Sample size was determined using data from our earlier studies (Hayward and Garton 1988). We calculated the minimum adequate sample necessary to reduce the coefficient of variation (CV) to 30–70% for measurements of tree density and cover in Douglas-fir forest and used this sample size for all vegetation types. The sample for each forest cover type also was similar in magnitude to our sample of owl nest locations.

*Nest Tree and Site Characteristics.*—At each nest site, we recorded characteristics of the nest cavity, nest tree, and forest immediately around the nest. Nest cavity measurements included entrance diameter (vertical and horizontal), cavity depth (vertical from base of cavity to bottom of entrance hole), cavity width, tree diameter at cavity, cavity aspect, and cavity height above the ground.

Forest structure immediately adjacent to the nest was described by measuring tree density, canopy cover, and basal area. We collected tree density data within a 5.2-m-circular plot and an outer donut (5.3–11.4 m) both centered on the nest tree. Trees were counted in 7 diameter classes: 2.5–7.6-cm, 7.7–15-cm, 15.1–23-cm, 23.1–38-cm, 38.1–53-cm, 53.1–68-cm, and >68-cm dbh (modified after James 1971). We also counted the number of snags in the

same diameter classes on the combined plots and estimated the height of the tallest tree in each plot. We measured overstory canopy cover using a modified, concave, forest densiometer (Lindsey 1956, Strickler 1959). Holding the densiometer at waist height, the number of 17 points obscured by foliage was counted 5 paces from the nest tree in each of 4 cardinal directions and while facing the tree 3 paces to the north. Percent canopy cover was calculated as the proportion of 85 points obscured by foliage. We measured basal area of trees >15-cm dbh using a relaskop and 20 factor angle centered at the nest tree. The nest tree was excluded from basal area calculations. We also recorded dominant tree species, canopy height, distance to nearest opening, distance to ecotone, and habitat type to phase (Steele *et al.* 1981).

*Roosting Habitat.*—We located owls on their daytime roosts through radio tracking. We tried to locate each owl twice each week during our field seasons. Measurements taken at each roost were designed to quantify the degree of cover provided by the roost tree and surrounding vegetation, to record site characteristics that would influence microclimate, and to classify the forest stand by habitat type (Steele *et al.* 1981).

While observing the roosting owl, we recorded compass aspect, slope (using a clinometer), topographic position, snow depth, dominant tree species (i.e., the most abundant species), and height to forest canopy. For the roost tree, we recorded roost tree species, dbh (measured with a reach stick [James 1971]), height of lowest foliage, tree crown diameter, tree height, perch height, and roost tree structure (open, closed, dense, or witch's broom [abnormally dense growth of foliage]). In addition, we recorded aspect of perch from bole, aspect the bird was facing, direction of wind (using a hand-held compass), wind speed at roost and in the open (using a hand-held anemometer), temperature at the roost and in the closest opening (both recorded 1.3 m above ground level, in shade, using a pocket thermometer accurate at 0.5 C), distance from the owl to the

bole, distance to nearest foliated branch above, below, and to the side of the owl, percent of cloud cover, and percent of snow cover in the open and under the canopy. Unless otherwise indicated, measurements were ocular estimates by trained observers (crew leaders worked with new technicians on at least 5 sites). We marked the tree so that it could be located for further habitat measurements.

In summer we returned to approximately 67% of the roost trees located during winter and summer to measure vegetation structure. To gather a sample from approximately 200 winter and 200 summer roosts, we systematically eliminated every third roost (ordered chronologically) for structural measurements. We collected tree density data within 2 concentric circles centered on the roost tree as described above (*see* Nest Tree and Site Characteristics). Tree size classes were modified by changing the 2 largest classes to 38.1–68 cm and >68 cm.

At 120 winter roosts and 123 summer roosts, we collected the same forest structure, topographic, and floristic data for a paired random tree. To locate the paired tree, we first spun a compass dial while looking away to determine the number of paces to travel (constrained to 30–180). A second compass spin indicated direction. After pacing off the distance in the designated direction, the closest tree >5-cm dbh became the new plot center.

### Nest Box Experiment

We examined the relative importance of vegetation structure and cavity availability to nest site selection by boreal owls with a nest box experiment. Forty-five wooden nest boxes hung by the authors in July 1984 within a 9-km<sup>2</sup> portion of the Chamberlain study area provided suitable nest structures in all forest vegetation types other than riparian forest stands (15 in mixed conifer, 11 in Douglas-fir, and 19 in lodgepole pine). Nest boxes (constructed from 2-cm-thick lumber) measured 44-cm high, 25-cm wide, 18-cm deep, and had a 9-cm-diameter entrance (modified from



R. A. Ryder, Colo. State Univ., pers. commun.). The boxes were hung in a rectangular grid with 500 m between grid points. Boxes were paired at each grid intersection to increase the probability that 1 box at each grid would be suitable for nesting each year. The paired boxes were placed 100 m apart and hung 4–15 m high. Boxes were placed on north or east sides of the tree bole unless overstory canopy would shade the box from afternoon sunshine. We checked and cleaned boxes of debris each year during June.

Three broad forest categories dominated the experimental area: old mixed-conifer forest (dominated by ponderosa pine), mature and older Douglas-fir, and mature lodgepole pine. Availability of natural cavities suitable for boreal owls varied in these types (G. D. and P. H. Hayward, pers. obs.) and in physiognomy. At Chamberlain, during 5 years of field work, we never saw a large cavity in lodgepole-pine forest and saw <10 in Douglas-fir stands. The paucity of cavities in Douglas-fir may result from the pattern of decay in Douglas-fir trees in this region (McClelland 1977). In contrast, a single hectare of mixed-conifer forest contained over 9 pileated woodpecker cavities in 1 instance. Our playback surveys throughout the experimental area also indicated significant differences in boreal owl nesting across the 3 forest vegetation types. Within the experimental area, we never observed nesting or a potential nesting attempt by boreal owls in lodgepole-pine forest and observed only a single nest site in Douglas-fir forest. In contrast nest trees and calling sites were located 6 times in mixed-conifer forests.

By hanging nest boxes in these 3 forest vegetation types (which differed in forest structure and cavity availability), we sought to differentiate the influence of cavity availability from forest structure in the choice of nest sites by boreal owls. If forest structure dominated the choice of nest site, we expected nest-box use to differ between lodgepole pine and the other forest vegetation types. If cavity availability (regardless of forest structure) was important to the owls, we expected to observe similar

use of nest boxes among the forest vegetation types.

In our experimental design, each forest vegetation type represented a treatment and each nest box was considered an independent observation repeated over a 4-year period (1985–88). An optimum level of interspersion among treatments was not possible because of the natural distribution of vegetation within the study area. Each forest vegetation type was distributed across the study area in large blocks. Therefore, nest boxes within a treatment (e.g., lodgepole-pine forest) were not completely interspersed with boxes in other treatments (this is a problem in any field experiment of this type) (Hurlbert 1984).

### Food Habits

We sampled prey being captured by boreal owls at Chamberlain each year during winter and summer by collecting regurgitated pellets at daytime roosts, identifying prey cached with roosting owls, and by identification of prey at nest sites. We thoroughly searched for regurgitated pellets under each roost tree while the bird was on the roost and again when we visited the site for vegetation measurements. Because boreal owls used different roosts each day, regurgitated pellets found beneath roost trees located through radio tracking could be assigned to individual owls and specific dates. Similarly, prey identified from nests while the female was incubating or brooding were attributed to the male. When the female ceased nest attendance, we used radiotelemetry to determine whether she was delivering prey to the nest and thereby assigned the prey to the appropriate owl.

Prey samples were recorded from nest sites by visiting nests weekly to identify fresh prey and collect prey remains. Fresh prey were identified at the nest and left for the owls to consume. Nest debris that included regurgitated bones, fur, feather, and insect chitin was collected during the visit for later identification. After air drying, the debris was carefully sorted by hand and all bones and feathers removed for

identification. Mammals were identified by dentition using reference collections of mammals captured on the study area and specimens at the University of Idaho, Department of Zoology, Museum. To avoid duplicate counting of fresh prey and debris, prey identified fresh was subtracted from those identified in the laboratory from debris before recording the total. Prey from pellets collected at roost sites were enumerated by dissecting the pellets and identifying prey as described for nest contents.

Frequency of occurrence for particular taxa in the diet of male and female owls was tallied within seasons by combining samples across years and owls using collections from roosts and nest sites. We examined differences among years and among individuals, but present the results elsewhere (Hayward 1989). To estimate the proportional biomass represented by each prey taxa, we multiplied prey frequency by estimated prey mass. Representative prey mass was determined by calculating the average mass of each mammal species captured during our small mammal investigations at Chamberlain. Estimates for northern pocket gophers (*Thomomys talpoides*) and northern flying squirrels (*Glaucomys sabrinus*) were taken from Hall (1946).

### Small Mammal Habitat Use and Relative Abundance

To estimate the relative abundance and species composition of small mammals and to discern any trend in small mammal abundance between years, we sampled small mammals at Chamberlain from 1984 to 1988 using methods similar to those employed in long-term studies of boreal owls in Scandinavia (Korpimäki 1984, Lofgren et al. 1986, Korpimäki and Norrdahl 1991). Samples consisted of snap-trapping grids run each spring and pit-trap sets established during spring 1985 and monitored through August 1988. The methodology was chosen to minimize time invested but provide an index of year-to-year population trends and an indication of habitats used by each small mammal species.

Rectangular 9 × 10 trapping grids of museum special traps spaced 15 m apart and baited with peanut butter and rolled oats were checked daily for 7 days each spring. The first trap grid was begun 19 May in 1984 and 1985, 26 May 1986, 22 May 1987, and 23 May 1988. In 1984, 1 grid was placed in each of 4 vegetation types: sagebrush-bunchgrass, *Carex* wet meadow, lodgepole-pine forest, and old mixed-conifer forest. We placed trapping grids in forest stands at least 30 m from an ecotone. In 1985, the same sites were trapped in the same order with 1 exception. The *Carex* wet meadow (a pasture used by U.S. Forest Service stock) was replaced with an adjacent, less disturbed meadow that was trapped each of the next 3 years. A second lodgepole-pine stand and a mature Douglas-fir forest site were added in 1985. All sites trapped in 1985 also were trapped in 1986 plus an additional old spruce-fir stand. These same 7 sites were trapped in 1987.

Pit-trap sets established on 18 sites in 1985 and 2 additional sets established in 1986 permitted sampling of numerous plots with a minimum investment of time. Each pit-trap set consisted of 4 cone-shaped, 40-cm-deep pits placed along a 3-m-long, 15-cm-high, sheet metal, drift fence (Williams and Braun 1983). One pit was located at the ends of the fence and 1 on either side at the center. Each pit was covered with sheet metal held 5 cm above the ground by corner stays. This cover prevented sticks, rain, and snow from entering the pit. Each metal pit contained 8 cm of 50% ethanol topped with mineral oil to preserve captured specimens. Traps were checked once each month from May to August and left functional through the winter.

Sites for pit-trap sets were chosen subjectively to distribute the traps throughout the Chamberlain study area and to sample 6 vegetation types: wet meadow, sagebrush-bunchgrass, subalpine-fir forest, lodgepole-pine forest, Douglas-fir forest, and mixed-conifer forest. Pit-trap sets sampled 3 stands in each of the 6 vegetation categories, except we placed 5 sets

in spruce-fir forest (2 in wet, old-spruce bottoms and 3 in mesic spruce-fir). Vegetation was measured at each site using methods described for owl breeding habitat. One pit-trap set was paired with each of the 6 snap-trap grids. The paired pit-trap sets were placed 30–70 m from the snap-trap grid within the same vegetation type.

## STATISTICAL ANALYSIS

Throughout our analysis, we divided each year into 2 periods (snow free and snow covered), which we refer to as summer and winter. The period of snow cover each year was defined as the period from January (when we began field work) until over 50% bare ground was exposed on level ground at 1,800 m (about 1 May). When reporting averages, confidence limits (CL) represent the 95% margin of error unless otherwise specified, and for hypothesis tests  $P < 0.05$  was considered significant unless otherwise noted.

We examined the pattern of population growth at the Chamberlain study site during 1984–87 using simple matrix projection models (Leslie 1945, Caswell 1989:15–26). Parameters for the models were estimated using vital rates from nests and radio-marked owls at Chamberlain.

## Boreal Owl Habitat Analysis

*Nesting Habitat RNRW.*—We compared the structure of forest vegetation in 101 stratified random forest stands with 33 boreal owl nesting or calling sites using Principal Component Analysis (PCA) (Stauffer and Peterson 1985, Digby and Kempton 1987). Prior to analysis, we plotted the frequency distributions of each structural variable at random sites and boreal owl use sites separately. Few approached a normal distribution and transformations of several variables failed to achieve normality. We calculated principal components without transforming variables, however, because Johnson and Wichern (1982:362) indicated that ordination by PCA does not require a multi-

variate normal assumption. Because we measured different characteristics of forest structure in different units (e.g., cover in %, density in no./ha), we transformed all variables to Z scores prior to analysis (Pielou 1984). We entered the 21 habitat variables measured on 101 stratified random forest sites into PCA. This analysis defined the principal component axes describing primary gradients of the forest habitats of the Chamberlain site. We then used the eigenvectors from this analysis to calculate principal component scores for boreal owl use sites. Finally, we plotted random and use sites along the gradients defined by the original PCA. The pattern was analyzed descriptively comparing the distribution of random sites and owl locations.

*Roost Habitat.*—To test for differences in forest structure between winter and summer roosts, we cast a 2-way MANOVA, blocking by owl. Through this analysis we controlled for the effect of individuals and could test for interactions among seasons and owls.

To test whether boreal owls chose roost sites with different microhabitat structure than forests in the vicinity of roosts, we used a multivariate paired-*T* test (Hotelling's  $T^2$ , Mendenhall et al. 1971, Johnson and Wichern 1982). The test was calculated separately for winter and summer. To do so, we subtracted the value for each of 20 structural variables measured at the roost from the corresponding values at the paired random site. We then tested whether the resulting mean vector differed significantly from a vector of zeroes. A significant result was used as justification to explore which individual structural variables differed between roosts and random sites (Johnson and Wichern 1982).

## Home Range and Owl Movements

Seasonal home range size and boundaries were calculated by the harmonic mean method using the program HOME RANGE (Samuel et al. 1985). We also calculated home range areas using a more conventional kernel method (Worton 1989), which employed an adaptive kernel



estimator (Silverman 1986). Although the adaptive kernel has desirable properties relative to the harmonic mean method (Worton 1989), it did not perform well with multimodal distributions. We considered the adaptive kernel estimates for several owls unrealistically large based on plots (over an order of magnitude greater than harmonic mean estimates) and therefore base our interpretations on the harmonic mean estimates. However, means for both estimators are reported.

Prior to home range analysis, we examined the input data for outliers (e.g., observations representing distant excursions from an owl's normal activity areas) (Samuel et al. 1985) and tested the influence of sample size on area estimates (see Hayward et al. 1987b). Extreme observations inevitably plague home range studies (Schoener 1981). Outliers in a bivariate test (Samuel et al. 1985), defined as those points with bivariate normal weights lower than 0.6, were considered for removal. If the point represented a movement to an area over 2 km from the owl's normal use area and was used for <3 days, the point was removed.

To describe daily movements and variation in seasonal movements, we calculated the distance between roost sites used on consecutive days and roost-to-nest distances. The sampling units were mean distances for individual owls during a season. The measurements of distances between roosts were considered subsamples, and mean distance between consecutive roosts (within seasons) was calculated from these values.

## RESULTS

### Regional Habitat Use

Outside the RNRW, 49 boreal owl nests or singing male owls were found during 130 surveys covering nearly 1,300 km of transect from 500 to 3,050 m elevation. Forest cover in survey areas ranged from ponderosa pine at the lower elevations to lodgepole pine and spruce-fir at the highest sites. All owl locations were in sub-

alpine-fir, Engelmann spruce, western hemlock (*Tsuga heterophylla*), and Douglas-fir habitat types (Steele et al. 1981) within the subalpine-fir life zone or within 100 m elevation of the subalpine-fir zone (Hayward et al. 1987a). Forest cover at owl locations outside the RNRW included lodgepole pine, Douglas-fir, western hemlock-western larch-subalpine fir, Engelmann spruce, and mixed spruce-fir.

The majority (88% of 49 observations) of owls were located in stands on subalpine-fir habitat types. Proportions for other habitat types included Engelmann spruce (3%), Douglas-fir (6%), and western hemlock (3%). Boreal owls were not heard below 1,292 m elevation, and 75% of the locations were above 1,584 m. Topographic position of owl locations ranged from bottoms to upper slopes.

Biologists classified 76% of the sites, where they heard boreal owls and could locate the stand the owl was using, as mature or older. The exceptions were lodgepole-pine stands on the Beaverhead National Forest in drainages where lodgepole was the only coniferous vegetation type. These lodgepole sites supported the largest trees in the area. On 1 lodgepole site, 404 trees/ha exceeded 23.1-cm dbh and 15/ha exceeded 53-cm dbh. Boreal owls were never heard singing in even-aged, young forest stands in drainages where mature forest stands were available. Over 50% of the boreal owl locations we visited outside the RNRW were marked for timber sale.

*Regional Microhabitat Use.*—We measured stand structure at 21 owl sites located by cooperating biologists in the region-wide survey. The sample included all sites located prior to August 1985 where the singing site could be assigned to a specific forest stand. Stands used by boreal owls in forests within the northern portion of the survey region had higher basal area and more large trees than stands used in the southern forests (Table 1). In both northern and southern areas, owls occurred predominantly in multistoried, old forest stands. On the Beaverhead National Forest where multistoried forest was not available, owls sang in even-aged lodgepole-pine

Table 1. Characteristics of forest structure measured at boreal owl singing sites located throughout the northern Rockies, 1984–85. We summarized northern forests (Maritime) separately from southern, dryer sites (Continental). Canopy cover is recorded in height categories above ground.

Structural feature	Maritime (n = 12)				Continental (n = 9)			
	$\bar{x}$	$\pm 95\%$ CL	Range	CV (%)	$\bar{x}$	$\pm 95\%$ CL	Range	CV (%)
Tree density (No./ha)								
2.5–7.6-cm dbh	740	476.5	30–2,543	102	387	164.7	150–793	56
7.7–15-cm dbh	298	149.7	15–853	80	284	59.7	164–419	28
15.1–23-cm dbh	101	52.3	0–314	82	204	104.6	75–478	68
23.1–38-cm dbh	131	54.2	45–329	66	176	87.5	0–374	66
38.1–53-cm dbh	62	19.9	25–125	51	43	23.4	6–94	72
>53-cm dbh	43	27.3	0–137	102	11	12.3	0–49	145
2.5–38-cm-dbh snags	118	96.7	0–464	129	111	79.8	0–314	98
>38-cm-dbh snags	35	20.3	0–112	92	13	9.9	0–80	205
Basal area (m <sup>2</sup> /ha)								
Trees >30.5-cm dbh	29.7	11.35	7.3–68.5	61	14.7	6.57	3.7–34.2	59
Tree canopy cover by height category (%)								
0–1 m	16	3.8	4–37	52	8	6.3	0–21	107
1.1–2 m	16	3.2	5–33	47	8	4.5	1–17	75
2.1–4 m	19	2.6	8–34	32	12	5.4	2–22	57
4.1–8 m	25	3.3	7–45	30	22	5.5	11–32	33
>8 m	30	6.0	7–52	46	28	12.7	12–65	58
Shrub canopy cover (%)	43	16.6	0–76	61	14	12.7	0–44	118
Ground cover (%)								
Forb	27	12.4	2–65	73	7	4.9	0–21	95
Grass	8	7.6	0–31	134	14	8.0	1–28	75
Subshrub	2	1.9	0–9	185	7	11.6	0–46	205

forest. These lodgepole stands were open and included large trees (>38-cm dbh). Density of trees over 23-cm dbh on 3 lodgepole-pine sites averaged 260/ha with 778 trees  $\leq$  23-cm dbh/ha. Aside from these lodgepole-pine sites, boreal owls were heard calling only from stands with components of old forest (more than 1 canopy layer, large trees, or more than 2 size classes of trees).

### Nesting Habitat Use in the RNRW

*Available Forest Structure.*—Prior to sampling stand structure, we subjectively classified forest vegetation within the study area into 4 cover types based on dominant overstory tree species—lodgepole pine, Douglas-fir, mixed conifer, and spruce-fir. Each type exhibited some distinct structural characteristics, whereas other structural features are not correlated with the overstory species (Table 2). For instance, overstory canopy cover did not vary across cover types, but basal area differed be-

tween lodgepole pine and other cover types. Thus, sites could not be adequately described simply through classification by overstory (Table 2). These results indicate that an analysis that relied only on classification of habitat (Allredge and Ratti 1986) would ignore important variation.

Principal components analysis (PCA) of 101 stratified random stands produced a description of the structural gradients available in the study area (Table 3). From 21 simple structure variables, PCA defined 6 components with eigenvalues >1, accounting for 75% of the overall variance. The seventh component accounted for less variance (4.75%) than would be expected for any one of the original variables.

We interpreted the principal components as gradients in vegetation structure and plotted sample sites along these axes (Fig. 3).

1. Component 1 describes a complex gradient from highly structured, mature and older forest with many canopy lay-

Table 2. Structural characteristics of 4 forest vegetation types in Chamberlain Basin, Idaho, measured on 25 randomly selected macroplots for each vegetation type, 1984–86. Vegetations were defined by dominant overstory trees.

Structural feature	Forest type							
	Lodgepole pine		Mixed conifer		Douglas-fir		Spruce-fir	
	$\bar{x}$	$\pm 95\%$ CL	$\bar{x}$	$\pm 95\%$ CL	$\bar{x}$	$\pm 95\%$ CL	$\bar{x}$	$\pm 95\%$ CL
Tree canopy cover by height category (%)								
0–1 m	2	1.2	3	0.7	6	1.4	16	3.5
1.1–2 m	2	1.3	6	1.3	10	1.5	15	3.0
2.1–4 m	5	1.8	12	2.5	16	2.7	19	2.5
4.1–8 m	13	3.7	25	4.0	28	3.5	25	3.1
>8 m	33	4.9	30	4.1	32	5.0	30	5.6
Shrub canopy cover (%)	1	1.1	1	0.6	4	3.1	6	3.2
Tree density (No./ha)								
2.5–7.6-cm dbh	387	150.2	308	162.0	1,040	361.5	935	212.4
7.7–15-cm dbh	284	54.5	255	72.2	443	171.6	530	115.3
15.1–23-cm dbh	204	95.4	147	40.6	178	30.1	337	79.4
23.1–38-cm dbh	176	79.9	77	24.2	111	25.6	193	34.2
38.1–53-cm dbh	4	4.0	17	5.5	28	13.6	32	10.1
>53-cm dbh			25	6.6	16	5.4	12	0.4
2.5–38-cm-dbh snags	111	74.7	73	30.1	211	136.8	194	31.5
>38.1-cm-dbh snags			7	6.4	2	1.4	12	8.3
Basal area (m <sup>2</sup> /ha)								
Trees >30.5-cm dbh	2.0	1.0	15.8	2.8	12.7	3.5	13.1	4.01

ers to young or aggradation stage forest with little vertical diversity. This component describes the overall physiognomy of the stand whereas subsequent components relate to individual features of forest structure (i.e., understory, overstory).

- Component 2 is a gradient with dense cover 0–2 m above the ground, numerous 2.5–15-cm-dbh trees and few large trees describing the positive end.
- Component 3 defines a cline in occurrence of large trees (>53-cm dbh), high basal area, and upper canopy cover.
- Component 4 defines a gradient in trees 15.1–38-cm dbh with a strong upper canopy.
- Component 5 includes stands with large snags (>38-cm dbh) and little grass cover.
- Component 6 is a gradient in forb ground cover.

A combination of principal Components 1 and 2 separates spruce-fir, lodgepole-pine, and mixed-conifer stands (Fig. 3). The simple structure of lodgepole-pine stands (compared to other types) is evident in Component 1, whereas spruce-fir and

mixed conifer differ most in understory cover (Component 2). Douglas-fir forest is dispersed throughout the gradient occupied by spruce-fir and mixed conifer. The striking differences between lodgepole-pine stands and other forests is lost when viewed along gradients defined by Components 3 and 4. Unlike some regions of the Rockies, multiple-canopy-layered lodgepole-pine forest is common in the study area.

*Relationship of Owl Use to Available Forest Structure.*—In this analysis, we examined whether boreal owls in the RNRW showed evidence of nonrandom use of nesting habitat. We analyzed the results of vegetation measurements at 21 nest sites and 12 calling sites to determine whether the owls restricted nesting to particular habitats. Boreal owl breeding locations were found in mixed-conifer (39.4%), spruce-fir (18.2%), Douglas-fir (21.2%), and aspen (21.2%) stands. Lodgepole pine, which covers over 50% of the study area, was the only abundant vegetation type not used for nesting. The proportion of use in each type, however, could not be compared to the available proportion because owl surveys were not designed to sample



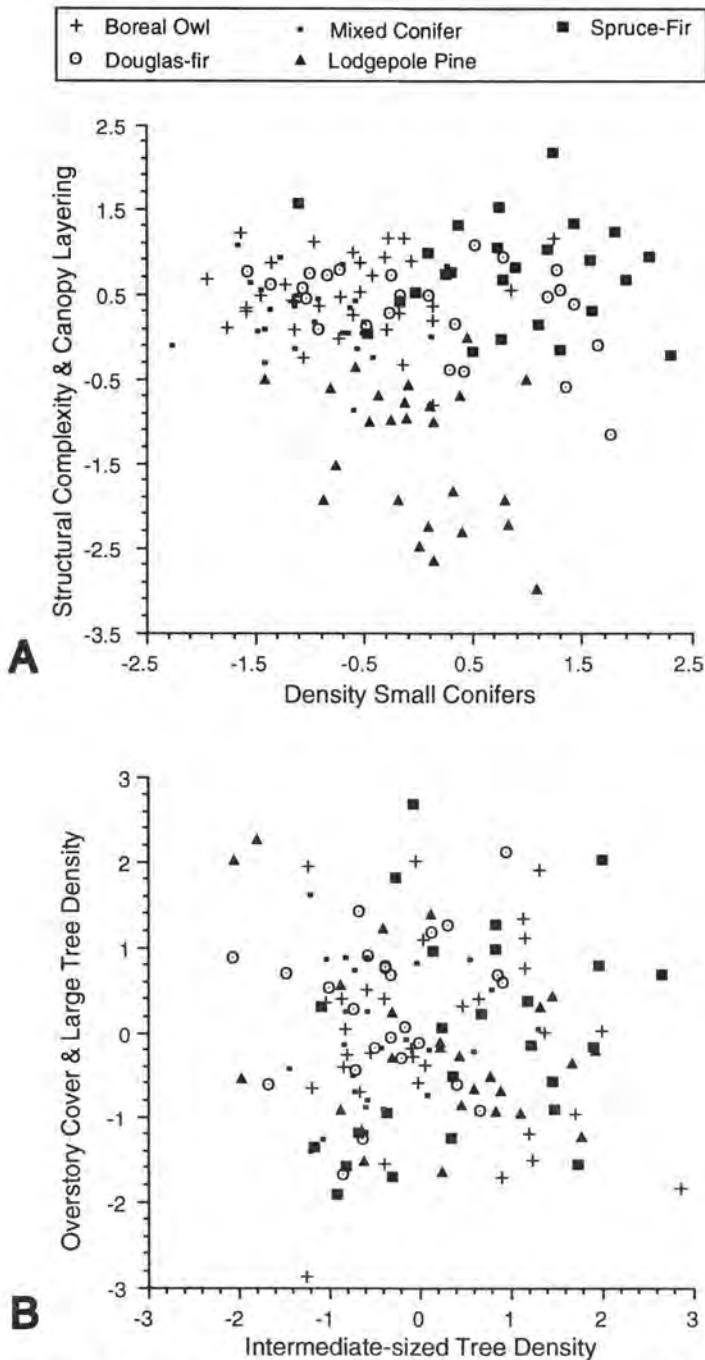


Fig. 3. Relationships among 4 vegetation cover types and boreal owl nest sites as defined by principal components analysis (PCA) of 21 forest structure variables. Each plot depicts the placement of 101 random plots and 33 boreal owl nest sites on 2 gradients defined by PCA. (A) Principal component 1 on Y-axis; principal component 2 on X-axis. (B) Principal component 3 on Y-axis; principal component 4 on X-axis.

Table 3. Six principal components derived from analysis of structural features measured at 101 random plots in 4 general vegetation types at Chamberlain Basin, Idaho, in 1985. Zero loading was 0.45 throughout.

Structural feature	Principal component					
	1	2	3	4	5	6
Basal area	0.668	-0.452	0.478			
Density trees 2.5-7.6-cm dbh		0.687				
Density trees 7.7-15-cm dbh	-0.733	0.481				
Density trees 15.1-23-cm dbh	-0.513			0.501		
Density trees 23.1-38-cm dbh				0.722		
Density trees 38.1-53-cm dbh	0.553					
Density trees >53-cm dbh	0.514	-0.487	0.477			
Density snags 2.5-38-cm dbh	-0.767					
Density snags >38-cm dbh					0.588	
Conifer cover 0-1 m	0.544	0.634				
Conifer cover 1.1-2 m	0.666	0.607				
Conifer cover 2.1-4 m	0.763					
Conifer cover 4.1-8 m	0.596					
Conifer cover >8 m			0.720	0.480		
Horizontal cover diversity	0.812					
Low conifer vertical diversity	0.605	0.745				
High conifer vertical diversity	-0.479		0.604			
Subshrub cover		0.467				
Grass cover					-0.555	
Forb cover						0.685
Eigenvalue	5.839	3.771	2.037	1.743	1.223	1.104
% variance explained	27.8	18.0	9.7	8.3	6.1	5.3
Cumulative %	27.8	45.8	55.5	63.8	69.9	75.2

types in proportion to their availability. Despite this problem, the high use of aspen, which accounted for <1% of forest vegetation cover, suggests strong selection for some components of aspen stands. The lack of nests in lodgepole-pine forest, which was surveyed more than other types, demonstrates avoidance of the most abundant vegetation type in the basin.

To compare vegetation structure at potential breeding sites and our random sites, we plotted boreal owl singing locations and nest sites with the stratified random sites on the first 4 principal components described above (Fig. 3). Owl sites were given a score on each principal component based on the vegetation analysis. The owl sites were then plotted in the space defined by the first 4 principal components of the vegetation analysis. The first 4 components accounted for 64% of the variance and were used to compare used sites with random sites. The resulting pattern indicates that boreal owls used structurally complex stands (Component 1) with less understory development than many available sites

(Component 2) (Fig. 3). The nonrandom pattern of owl use on axes 1 and 2 contrasts with the pattern observed on subsequent axes. Owl sites included stands with a range of overstory cover and large tree densities (Component 3) closely matching the full range of available types. Likewise, owl use sites were scattered across the gradient describing large tree density (Component 4) (Fig. 3).

*Description of Owl Breeding Sites in RNRW.*—The above analysis suggests that boreal owls choose nest sites in a nonrandom manner; the physiognomy of owl use sites did not encompass the full range of available types. Nesting and calling sites never occurred in dense, even-age forest, and boreal owls never nested in lodgepole-pine forest—the most abundant cover type in the study area. Relative to stratified random sites, the most characteristic structural features of 33 nesting and calling sites were a high density of large trees (>38-cm dbh), open understory, and a multi-layered canopy (Table 4).

All but 2 of 23 nests were in trees within

Table 4. Characteristics of forest structure measured at 33 boreal owl calling and nest sites in the Frank Church River of No Return Wilderness during 1984–88. Canopy cover is recorded in layers above the ground.

Structural feature	$\bar{x}$	$\pm 95\%$ CL	Range	CV (%)
Tree density (No./ha)				
2.5–7.6-cm dbh	450	140	29–1,795	91
7.7–15-cm dbh	298	86	82–1,226	85
15.1–23-cm dbh	162	40	15–434	72
23.1–38-cm dbh	126	31	15–320	72
38.1–53-cm dbh	34	10	0–141	86
>53-cm dbh	23	6	0–64	76
2.5–38-cm-dbh snags	115	49	0–763	126
>38-cm-dbh snags	9	6	0–91	202
Basal area (m <sup>2</sup> /ha)				
Trees >30.5-cm dbh	17.8	3.1	3.7–40.9	51
Tree canopy cover by height category (%)				
0–1 m	6	1.7	1–2	84
1.1–2 m	8	1.3	1–16	47
2.1–4 m	13	2.1	5–27	47
4.1–8 m	22	3.2	2–41	43
>8 m	30	4.3	4–5	42
Ground cover (%)				
Forb	12	4.0	1–55	73
Grass	8	3.1	4–50	50
Subshrub	7	27.0	0–26	111

a forest stand. One unusual nest occupied a lone spruce in a small boulder field. An extensive stand of large spruce and fir trees lay 16 m to the south of the 71-cm-dbh spruce. This nest failed 15 days after hatching 3 young. The second unusual nest was in a Douglas-fir snag in a 0.5-ha island of mature trees 20 m from extensive spruce–fir forest.

To describe forest stand sizes chosen for nesting, we estimated the area of the nest stand from the size of the area surrounding the nest tree that was characterized by homogeneous tree species and tree size class. Nest stands ranged from 0.8 to 14.6 ha and averaged  $7.6 \pm 3.96$  ha. All 5 aspen nest stands ranged between 0.8 and 1.3 ha, whereas the smallest coniferous-forest nest stand covered 1.6 ha. All of these stands were surrounded by forest.

*Nest Box Experiment.*—During 4 years, owls were observed courting or nesting at only 3 nest boxes in the experiment. Al-

though radio-tagged boreal owls frequently foraged and roosted near boxes in lodgepole pine, none nested there. In 1987, a pair of radio-marked owls fledged 2 young from a box in mixed conifer. A second box in mixed conifer fledged 2 young in 1988. In 1987, boreal owls nested in a box in Douglas-fir forest.

*Nest Tree Characteristics.*—During intensive studies in the RNRW, we found 23 boreal owl nests. Locating nests other than those used by radio-marked females was difficult. We found 6 nests occupied by unmarked owls, 2 of these in nest boxes. We found 3 nests when only the male member of the pair was radio marked and failed to find a nest for 6 radio-marked males. For the remaining 14 nests, either the female or both owls were radio marked.

We attributed the excavation of 18 of 19 natural nest cavities to pileated woodpeckers; a northern flicker probably excavated the other. Boreal owl nest-cavity



entrances averaged  $102 \pm 12.41$  mm high (range 64–150 mm) and  $95 \pm 11.89$  mm wide (range 56–148 mm). Nest cavity condition ranged from recently constructed cavities without a feces layer (indicating no prior nesting by woodpeckers or other birds) to old cavities with a deep layer of dried feces, cone scales, and other debris. Inside, the cavities ranged from 7 to 50 cm deep ( $\bar{x} = 31 \pm 7.61$  cm) and from 15 to 26 cm diameter ( $\bar{x} = 19 \pm 2.11$  cm). The tree diameter at the cavity averaged  $41 \pm 5.21$  cm (range 26–61 cm). Tree dbh averaged  $64 \pm 11.02$  cm (range 33–112 cm).

Excluding nests in nest boxes, owls nested in ponderosa pine 10 times (53%), aspen 7 times (37%), and once each in Douglas-fir (5%) and Engelmann spruce (5%). Ten nests occupied snags, including 8 ponderosa pine, 1 aspen, and 1 Douglas-fir. Snag condition included 3 old branchless snags >11 m tall, 2 hard snags with sloughing bark and only large branches remaining, and 5 young snags with bark and complete limbs. Among nests in live trees, all but 2 cavities occurred in an open area on the tree bole; distance to foliage above the cavity averaged  $3.8 \pm 1.67$  m (minimum 0.3 m). Over 75% of the cavities in live trees had no foliage below the cavity. For those that did, the minimum distance to foliage below was 0.6 m.

The owls chose relatively high cavities, averaging  $12.7 \pm 2.98$  m and ranging from 6 to 25 m. Cavity height averaged 51% of tree height. Boreal owl nests in snags or trees with multiple cavities always occupied 1 of the uppermost cavities suggesting a preference for high nest sites.

The forest immediately around nest trees had an open structure. Density of 2.5–23-cm-dbh trees within a 0.01-ha plot around the nest tree averaged  $398 \pm 162$ /ha (range 0–1,482) (Table 5). The density of trees at nests was 3 times lower than the average at winter roost sites. Density of trees larger than 23.1-cm dbh averaged  $212 \pm 86$ /ha, similar to average densities measured at winter roost sites.

Nest sites occupied forest stands in 3

Table 5. Forest structure at 19 different nest trees used by boreal owls in the Frank Church River of No Return Wilderness during 1984–88. Tree densities are reported for 2-concentric circular plots—an inner circle 5.2-m radius and an outer "donut" extending from 5.2 m to 11.4 m.

Site characteristic	$\bar{x}$	$\pm 95\%$ CL
Tree density (No./ha)		
Inner plot		
2.5–7.6-cm dbh	174	111.9
7.7–15-cm dbh	98	48.1
15.1–23-cm dbh	114	60.1
23.1–38-cm dbh	136	73.7
38.1–68-cm dbh	60	42.5
>68-cm dbh	11	15.6
Outer plot		
2.5–7.6-cm dbh	242	107.3
7.7–15-cm dbh	178	70.1
15.1–23-cm dbh	124	49.5
23.1–38-cm dbh	130	56.6
38.1–68-cm dbh	51	25.0
>68-cm dbh	10	7.8
Snag density (No./ha)		
2.5–38-cm dbh	79	42.2
>38-cm dbh	10	11.5
Basal area (m <sup>2</sup> /ha)	33.7	3.62
Canopy cover (%)	55	7.7
Topographic features		
Distance to water (m)	201	98.9
Slope (%)	28	5.8

habitat series (based on Steele et al. 1981). We found 17% of nest sites in Engelmann spruce (*Picea engelmannii*) series, specifically the Engelmann spruce-common horsetail (*Equisetum arvense*) habitat type; 39% in the subalpine-fir series, specifically subalpine fir-twisted stalk (*Streptopus amplexifolius*), subalpine fir-bluejoint (*Calamagrostis canadensis*), subalpine fir-beargrass (*Xerophyllum tenax*), and subalpine fir-grouse whortleberry (*Vaccinium scoparium*) habitat types; and 44% in the Douglas-fir habitat series, specifically Douglas-fir-common snowberry (*Symphoricarpos albus*), Douglas-fir-pinegrass (*Calamagrostis rubescens*), and Douglas-fir-elk sedge (*Carex geyeri*) habitat types. The slope at the nest ranged from flat to 49%, averaging  $28 \pm 6\%$ . Nest trees were distributed relatively evenly from bottoms

Table 6. Habitat types (Steele et al. 1981) of 194 winter and 342 summer roost sites used by boreal owls at Chamberlain Basin, Idaho, during 1984–87. We combined rare habitat types with those of similar moisture and structural characteristics.

Habitat types	Roost sites			
	Winter		Summer	
	No.	%	No.	%
Douglas-fir–blue huckleberry ( <i>Pseudotsuga menziesii</i> – <i>Vaccinium globulare</i> )	4	2.1	3	0.9
Douglas-fir–warm sites with ponderosa pine ( <i>Pinus ponderosa</i> ) codominant in the overstory <sup>a</sup>	45	23.2	6	1.7
Douglas-fir–pinegrass ( <i>Pseudotsuga menziesii</i> – <i>Calamagrostis rubescens</i> )				
Douglas-fir–white spirea ( <i>Pseudotsuga menziesii</i> – <i>Spiraea betulifolia</i> )				
Douglas-fir–Oregon grape ( <i>Pseudotsuga menziesii</i> – <i>Berberis repens</i> )				
Subalpine fir–hydric sites with lush understory of herbs and grasses <sup>a</sup>	12	6.2	16	4.7
Subalpine fir–twisted stalk ( <i>Abies lasiocarpa</i> – <i>Streptopus amplexifolius</i> )				
Subalpine fir–bluejoint ( <i>Abies lasiocarpa</i> – <i>Calamagrostis canadensis</i> )				
Subalpine fir–Canby's ligusticum ( <i>Abies lasiocarpa</i> – <i>Ligusticum canbyi</i> )				
Subalpine fir or Douglas-fir–cold air drainage sites with a sparse understory of short shrubs <sup>a</sup>	25	12.9	2	0.9
Subalpine fir–dwarf huckleberry ( <i>Abies lasiocarpa</i> – <i>Vaccinium caespitosum</i> )				
Douglas-fir–dwarf huckleberry ( <i>Pseudotsuga menziesii</i> – <i>Vaccinium caespitosum</i> )				
Subalpine fir–twinflower ( <i>Abies lasiocarpa</i> – <i>Linnaea borealis</i> )	9	4.6	5	1.5
Subalpine fir–mesic sites with tall shrubs <sup>a</sup>	9	4.6	8	2.3
Subalpine fir–Sitka alder ( <i>Abies lasiocarpa</i> – <i>Alnus sinuata</i> )				
Subalpine fir–menziesia ( <i>Abies lasiocarpa</i> – <i>Menziesia ferruginea</i> )				
Subalpine fir–high elevation mesic sites <sup>a</sup>	54	27.9	278	81.1
Subalpine fir–beargrass ( <i>Abies lasiocarpa</i> – <i>Xerophyllum tenax</i> )				
Subalpine fir–blue huckleberry ( <i>Abies lasiocarpa</i> – <i>Vaccinium globulare</i> )				
Subalpine fir–white spirea ( <i>Abies lasiocarpa</i> – <i>Spiraea betulifolia</i> )				
Subalpine fir–harsh, high elevation, mesic sites with understory of short shrubs and grasses <sup>a</sup>	11	5.7	12	3.5
Subalpine fir–grouse whortleberry ( <i>Abies lasiocarpa</i> – <i>Vaccinium scoparium</i> )				
Subalpine fir–elk sedge ( <i>Abies lasiocarpa</i> – <i>Carex geyeri</i> )				
Subalpine fir–heartleaf arnica ( <i>Abies lasiocarpa</i> – <i>arnica cordifolia</i> )				
Subalpine fir–pinegrass ( <i>Abies lasiocarpa</i> – <i>Calamagrostis rubescens</i> )	25	12.9	12	3.5

<sup>a</sup> Represents sum of habitat types listed immediately below

Table 7. Seasonal boreal owl roost characteristics measured at Chamberlain Basin, Idaho, during 1984–87. Tree densities were sampled from 2-concentric circular plots around the roost site. The inner circle was 0.0084 ha and outer "donut" was 0.0321 ha.

Variable	Season			
	Winter (n = 189)		Summer (n = 241)	
	̄	±95% CL	̄	±95% CL
Canopy cover (%)	58.5	1.91	63.5	1.54
Basal area (m <sup>2</sup> /ha)	26.0	2.03	29.8	1.87
Roost tree dbh (cm)	27.7	2.21	25.7	1.65
Tree density (No./ha)				
2.5–7.6-cm dbh—inner	797	120.5	1,380	142.4
2.5–7.6-cm dbh—outer	864	119.6	1,233	98.6
7.7–15-cm dbh—inner	561	81.3	897	78.8
7.7–15-cm dbh—outer	641	74.5	869	66.5
15.1–23-cm dbh—inner	261	32.0	341	33.5
15.1–23-cm dbh—outer	287	26.3	359	23.2
23.1–38-cm dbh—inner	130	20.2	181	21.3
23.1–38-cm dbh—outer	156	16.4	199	13.9
>38-cm dbh—inner	35	11.5	27	7.1
>38-cm dbh—outer	38	7.9	34	67.2
Snag density (No./ha)				
2.5–15-cm-dbh snags <sup>a</sup>	305	53.0	269	44.5
15.1–38-cm-dbh snags	37	7.9	49	8.8
>38-cm-dbh snags	2	1.2	8	2.4

<sup>a</sup> Snags measured in 0.04-ha-circular plot.

to upper slope positions (27% bottoms, 18% lower third, 14% midthird, 41% upper third). We failed to locate any nests on ridges.

### Roost Habitat and Roosting Behavior

Unlike many species of owls, boreal owls roost at sites throughout their home range; rarely do they roost in the same stand on consecutive nights. We located consecutive daytime roosts of 14 owls on 159 occasions. In only 8 cases did owls use the same tree on consecutive days.

*Pattern of Roost Habitat Use During Winter and Summer.*—Habitat type of roost stands differed between seasons ( $\chi^2 = 167.6$ ,  $df = 7$ ,  $P < 0.001$ ) (Table 6) reflecting the use of more moist, higher elevation sites in summer. The topographic position of roost sites also differed between seasons ( $\chi^2 = 63.7$ ,  $df = 6$ ,  $P < 0.001$ ). Boreal owls roosted in bottoms significantly more often in winter (27 vs. 9%) than in summer and on mid- and upper

slopes significantly more often in summer (12 vs. 26% midslopes, 29 vs. 41% upper slopes) than in winter.

We measured habitat structure at 430 roost sites of 24 radio-marked owls. Typical forest stands used for winter roosts had nearly 60% canopy cover, 26 m<sup>2</sup>/ha basal area, 1,620 trees/ha having 2.5–23-cm dbh, and 165 trees/ha over 23.1-cm dbh (Table 7). Although similar to winter roosts, summer roosts (on average) occurred in more dense forest with greater cover. Microhabitat at roosts in winter and summer was different (MANOVA Wilks'  $F = 5.2$ ;  $df = 7$ , 378;  $P = 0.0001$ ) mainly due to differences in density of trees 2.5–23-cm dbh (Table 8). Winter and summer roosts differed in all aspects of forest structure measured. Individual boreal owls also differed significantly in roost habitat (MANOVA Wilks'  $F = 2.34$ ;  $df = 154$ , 2,544;  $P = 0.0001$ ) although the smaller  $F$  value indicates less evidence for an effect than the difference in seasons (Table 8). Individual owl roost sites differed most in the density of large trees, canopy height, and basal area. The effects of individual owl and



Table 8. Multivariate analysis of variance examining seasonal differences in boreal owl roost site characteristics measured at Chamberlain Basin, Idaho, during 1984–87. Sites from individual owls are treated as blocks and the interaction (season  $\times$  owl) is included in the model. Univariate  $F$  and  $P$  values (based on type 1 sums of squares) suggest the roost characteristics most responsible for the significant seasonal effect (the "season"  $F$  and  $P$  values are included for the univariate summary). Tree density is estimated from an inner circle of 0.0084 ha and an outer "donut" of 0.0321 ha.

Source of variation	$F$	df	$P$
MANOVA (Wilks')			
Season	5.201	7; 378	<0.001
Owl	2.338	154; 2,544	0.001
Season $\times$ owl	1.145	119; 2,474	0.139
ANOVA for individual variables			
Canopy height	30.74	1	<0.001
Canopy cover (%)	16.96	1	<0.001
Basal area (m <sup>2</sup> /ha)	8.30	1	0.004
Tree density (No./ha)			
2.5–23-cm dbh—inner	47.70	1	<0.001
2.5–23-cm dbh—outer	33.28	1	<0.001
23.1–68-cm dbh—inner	6.76	1	0.009
23.1–68-cm dbh—outer	13.91	1	<0.001

season did not interact ( $P = 0.139$ ) indicating that the owl population as a whole consistently shifted roost habitat between seasons.

Unfortunately, finding an unequivocal answer to the question, "Does roost habitat differ between seasons?" is not straightforward. As we will show later, owls shifted home range slightly between winter and summer. Therefore, differences between seasons in roost habitat structure could result from changes in the range of available sites. To test whether shifts in home range

would confound any conclusions about microhabitat use, we evaluated seasonal differences in the paired random sites measured in conjunction with the owl roost sites. This analysis included only the random, not the used sites. Any difference in microhabitat resulting from seasonal shifts in home range also should be apparent in the paired random plots. The random plots, then, act as a control for the confounding variable, home range shift.

The results support the assertion that owl roost habitat differs between summer

Table 9. Multivariate analysis of variance examining seasonal differences in paired-random roost-site characteristics. Random sites from individual owls are treated as blocks and the interaction (season  $\times$  owl) is included in the model. Univariate  $F$  and  $P$  values (based on type 1 sums of squares) suggest the roost characteristics most responsible for the significant seasonal effect (the "season"  $F$  and  $P$  values are included for the univariate summary). Tree density is estimated from an inner circle of 0.0084 ha and an outer "donut" of 0.0321 ha.

Source of variation	$F$	df	$P$
MANOVA (Wilks')			
Season	1.630	7; 198	0.129
Owl	1.652	133; 1,318	0.001
Season $\times$ owl	1.162	56; 1,071	0.198
ANOVA for individual variables			
Canopy height	1.36	1	0.245
Canopy cover (%)	2.59	1	0.109
Basal area (m <sup>2</sup> /ha)	0.01	1	0.912
Tree density (No./ha)			
2.5–23-cm dbh—inner	6.56	1	0.011
2.5–23-cm dbh—outer	19.03	1	<0.001
23.1–68-cm dbh—inner	0.65	1	0.420
23.1–68-cm dbh—outer	3.35	1	0.068

Table 10. Comparison of vegetation characteristics at roost sites at Chamberlain Basin, Idaho, with paired-random sites in winter ( $n = 120$ ) and summer ( $n = 123$ ) during 1984–87. Mean difference expressed as roost minus paired-random site. Tree density is estimated from an inner circle of 0.0084 ha and an outer "donut" of 0.0321 ha.

Variable	Winter			Summer		
	$\bar{x}$ difference	SE	<i>P</i>	$\bar{x}$ difference	SE	<i>P</i>
Canopy cover (%)	6.05	1.704	<0.001	7.59	1.503	<0.001
Basal area (m <sup>2</sup> /ha)	12.20	6.774	0.07	11.80	5.801	0.04
Tree density (No./ha)						
2.5–7.6-cm dbh—inner	0.62	0.824	0.46	2.88	0.778	0.01
2.5–7.6-cm dbh—outer	2.52	2.902	0.39	-0.54	2.591	0.83
7.7–15-cm dbh—inner	0.68	0.529	0.21	1.20	0.545	0.03
7.7–15-cm dbh—outer	1.63	1.764	0.36	0.28	1.759	0.88
15.1–23-cm dbh—inner	-0.15	0.242	0.54	0.21	0.261	0.42
15.1–23-cm dbh—outer	-0.97	0.648	0.14	0.51	0.751	0.50
23.1–38-cm dbh—inner	0.21	0.159	0.19	0.44	0.142	<0.001
23.1–38-cm dbh—outer	0.55	0.404	0.18	0.82	0.321	0.01
38.1–53-cm dbh—inner	0.06	0.054	0.29	0.01	0.049	0.87
38.1–53-cm dbh—outer	0.18	0.166	0.30	0.07	0.132	0.62
53.1–68-cm dbh—inner	0.08	0.037	0.05	0.00	0.028	1.00
53.1–68-cm dbh—outer	0.08	0.051	0.15	0.00	0.057	1.00
>68-cm dbh—inner	0.03	0.021	0.10	-0.02	0.011	0.16
>68-cm dbh—outer	-0.06	0.054	0.29	-0.05	0.025	0.06
Snag density (No./ha)						
2.5–7.6-cm-dbh snags <sup>a</sup>	0.09	1.432	0.95	1.76	1.293	0.18
7.7–15-cm-dbh snags	-0.55	0.327	0.10	-0.35	0.313	0.27
15.1–23-cm-dbh snags	-0.39	0.177	0.03	-0.24	0.246	0.34
23.1–38-cm-dbh snags	0.28	0.114	0.01	-0.04	0.171	0.81
38.1–53-cm-dbh snags	0.00	0.031	1.00	0.07	0.068	0.34
53.1–68-cm-dbh snags	0.05	0.026	0.06	0.02	0.025	0.53
>68-cm-dbh snags	-0.02	0.021	0.42	0.01	0.008	0.32

<sup>a</sup> Snags measured in 0.04-ha-circular plot.

and winter (Table 9). No seasonal effect (MANOVA Wilks'  $F = 1.63$ ;  $df = 7, 198$ ;  $P = 0.129$ ) or significant interaction between season and owl (MANOVA Wilks'  $F = 1.16$ ;  $df = 56, 107$ ;  $P = 0.198$ ) appeared among random plots. The influence of individual owls was still apparent in the paired random plots (MANOVA Wilks'  $F = 1.65$ ;  $df = 133, 1,318$ ;  $P = 0.0001$ ) but was rather weak judging by the low  $F$  value. An unbalanced sample across individuals may have contributed to the low  $F$ ; however, the large number of degrees of freedom in this analysis suggests good power to detect even small differences in season—thus, we are confident in concluding that random plots showed no seasonal effect.

**Roost Habitat Selection.**—We located 882 roost sites from 1984 to 1987 and measured forest structure at 430 sites (Table 7). In both winter and summer, roost sites

differed significantly from paired random sites (Hotelling's  $T^2$ ; winter  $F = 2.04$ ;  $df = 120, 106$ ;  $P = 0.021$ ; summer  $F = 3.75$ ;  $df = 120, 106$ ;  $P < 0.0001$ ). Winter roosts had significantly greater canopy cover, more 23.1–38-cm-dbh snags in the inner plot, and fewer 15.1–23-cm-dbh snags than paired random sites (Table 10). Summer roosts had greater canopy cover, higher basal area, denser 2.5–15-cm-dbh trees in the inner plot, and denser 23.1–38 cm trees in both plots than paired random sites (Table 10).

Thus, we have stronger evidence for selection in summer than winter. Characteristics of summer roosts indicate the owls choose dense, shaded sites compared to paired random locations. When we compared temperature at the roost and in the nearest opening (both temperatures taken in the shade while the owl was roosting), roost sites were significantly cooler when



Table 11. Temperature differences between roost site and a nearby opening by temperature class for sites located in Chamberlain Basin, Idaho, during 1984–87. The negative mean difference indicates the roost was cooler than the paired reading.

Temperature in open (C)	n	$\bar{x}$ difference	SE of mean	$t^a$	P
1–4	80	-0.07	0.04	1.69	0.10
4.1–10	101	-0.18	0.07	2.62	0.010
10.1–15	99	-0.39	0.09	4.13	<0.001
15.1–21	125	-0.56	0.09	5.82	<0.001
>21	80	-0.98	0.12	7.93	<0.001

<sup>a</sup> Student's *t*.

ambient temperatures exceeded 4 C. The difference in temperature increased with increasing ambient temperature (Table 11).

*Roost Perch Characteristics.*—During winter, boreal owls typically perched  $7.2 \pm 0.21$  m high in a  $27 \pm 0.9$ -cm-dbh tree ( $n = 261$ ). The ratio of perch height to the tree height averaged 0.4 (75% of winter roosts occurred in the lower half of the tree, 25% in the lowest quarter). Only 25% of the time did owls roost at or below the height of the lowest foliage. Seventy percent of roosts occupied the dominant tree species in the stand. When the owl had cover within 5 m of the perch, the distance to foliage above the owl averaged  $0.8 \pm 0.15$  m, distance to foliage below averaged  $0.7 \pm 0.15$  m, and distance to foliage at the side averaged  $0.3 \pm 0.06$  m.

In summer, boreal owls continued to roost in the dominant tree species of the stand (66% of 378 roosts were in dominant tree species). Birds perched at a mean height of  $5.9 \pm 0.16$  m in  $25 \pm 0.7$ -cm-dbh trees. Fifty percent of roosts occurred in the lower third of the roost tree. As in winter, 25% of the summer roosts occurred at or below the height of the lowest foliage. When the owl had cover within 5 m of the perch, the distance to foliage averaged  $1.1 \pm 0.14$  m above the owl,  $0.7 \pm 0.10$  m below, and  $0.4 \pm 0.06$  m to the sides.

*Roosting Behavior.*—Daytime was a period of reduced activity for boreal owls. During daylight the owls spent the majority of time perched, eyes closed. On 16 occasions when we watched owls during daylight for 2 hours or more (total 46 hrs)

they perched quietly with eyes closed 77% of the time. Periods of sleep rarely lasted more than 40 minutes before being interrupted by brief (2–5 min) periods of preening or actively looking about. The owls spent 6% of the observation period preening. The birds preened plumage and feet, stretched wings, and on some occasions shook the entire plumage. Except for the extended preening bout of 20–30 minutes, which always preceded leaving the roost to begin foraging at night, the owls preened only a small portion of the plumage during a preening bout.

In addition to preening and sleeping, owls spent 10% of the day actively looking around and 4% of the time eating. Hunting during daylight (1% of observation period) and simply moving from 1 roost perch to another (1%) encompassed only a short portion of the daytime activity but may be important. Owls exhibited gullar fluttering during 1% of the 46 hours of observation (occurred only on warmer days).

Boreal owls frequently consumed prey during the daytime. Our observations suggest that few (*see below*) of the prey eaten at the daytime roost were captured from the roost. We saw owls retrieve cached prey and eat some portion of the prey on 63 occasions, and we noted prey cached near roosting owls on 20 other occasions. Cached prey was usually stored in the fork of a tree branch.

Boreal owls tended to eat or possess cached prey more frequently in summer than winter. We observed owls with cached prey at 17% of summer roosts and 4% of winter roosts ( $\chi^2 = 56$ ,  $df = 1$ ,  $n = 822$ ,  $P = 0.00001$ ). During summer the owls ate cached prey most frequently between 1200 and 1400 hours; 65% of observations of owls consuming cached prey occurred between 1120 and 1330 hours. In winter, we observed boreal owls eating prey throughout the day, although 66% occurred after noon. The distribution of observed feeding times differed from the distribution of our observed roost (radio tracking) location times for both winter and summer (winter  $\chi^2 = 6.3$ ,  $df = 3$ ,  $P = 0.097$ ; summer  $\chi^2 = 7.7$ ,  $df = 5$ ,  $P = 0.176$ ). For both tests we



chose  $\alpha = 0.20$ , which is conventional for goodness-of-fit tests (White *et al.* 1982).

When feeding on prey at the roost, boreal owls rarely consumed prey whole. In fact, over half of cached prey observed at roosts were headless. The owls often consumed the forward half of the prey in pieces. On 4 occasions we saw the owl extract the intestines from the abdominal cavity and discard them before proceeding to consume the rear half of the prey. The rear half of mice and voles were then consumed whole.

Boreal owls seldom foraged for an extended period during daylight. On only 1 of 16 days (46 hrs), when we watched roosting owls for over 2 hours at their roost, did an owl begin hunting. The owl foraged for 15 minutes. In conjunction with our ordinary roost observations, we observed the owls on 882 occasions. On 13 days (2.9%) in winter and 33 days (7.4%) during summer, the owl began foraging in daylight during the normal ~1-hour observation period at the roost. We observed owls attack prey from their roost tree (excluding instances of extended daytime foraging) on 7 occasions.

Boreal owls moved to a different roost tree more frequently than they hunted during daylight. Owls moved during our roost observations on 16% of the days during summer and 8% in winter. These roost changes were distinguished from foraging by the lack of rapid head turning after the move and frequently by the owl closing its eyes soon after the flight. Most often the owl moved to an adjacent tree and rarely flew over 40 m.

Boreal owls normally roost alone and, as discussed in the section on movements, usually roost far from the nest and their mate. Although we radio marked both members of 5 mated pairs prior to nesting, we observed the owls roosting within 150 m of one another during the prenesting period on only 5.8% of the occasions ( $n = 121$ ). One pair was found roosting together 4 times. On 14 March they roosted in adjacent trees 6.5 km from a nest site at which they had been courting since early February. The next day they again roosted

within 30 m of each other, but this time about 200 m from the nest. On 18 March they roosted together 2.6 km from the nest although they had not been together the previous day or early the previous evening. On 27 March the pair roosted within 30 m of each other 3 km from the nest and were together near the nest by 2145 hours. This behavior suggests that these 2 owls traveled together during some nighttime movements, remaining together during journeys as far as 6.5 km.

We found unmated radio-marked owls roosting together twice. On 1 May 1986, 2 males roosted 120 m from each other on a hillside used often by both owls. On 29 June 1987, a female who was caring for nestlings roosted within 150 m of a male who had not bred that year. Within 5 days the 2 owls' roosts were no closer than 10 km.

## Movements and Home Range Use

*Daily Movements and Distance Covered.*—Boreal owls lead a very mobile existence during both winter and summer. Although the limitations of travel within the wilderness prevented us from effectively following radio-marked owls during their foraging (Hayward 1987), locations of daytime roosts suggest the magnitude of the owls' daily movements. We used locations of consecutive daytime roosts and roost-to-nest distances as indications of the minimum travel distances. Although both measures certainly underestimate daily movement (Laundre *et al.* 1987), these indices do provide insight into the pattern of owl movements by describing minimum distances traversed.

We recorded distances between consecutive daytime roosts of 14 owls (7 females and 7 males) on 150 occasions over 4 years. Distance between roosts on consecutive days ranged from 0 to 6,935 m. Mean distances did not differ significantly between winter and summer (winter  $\bar{x} = 1,540 \pm 446$  m, summer  $\bar{x} = 934 \pm 348$  m). For this comparison we treated each radio-marked owl as a sample and consecutive

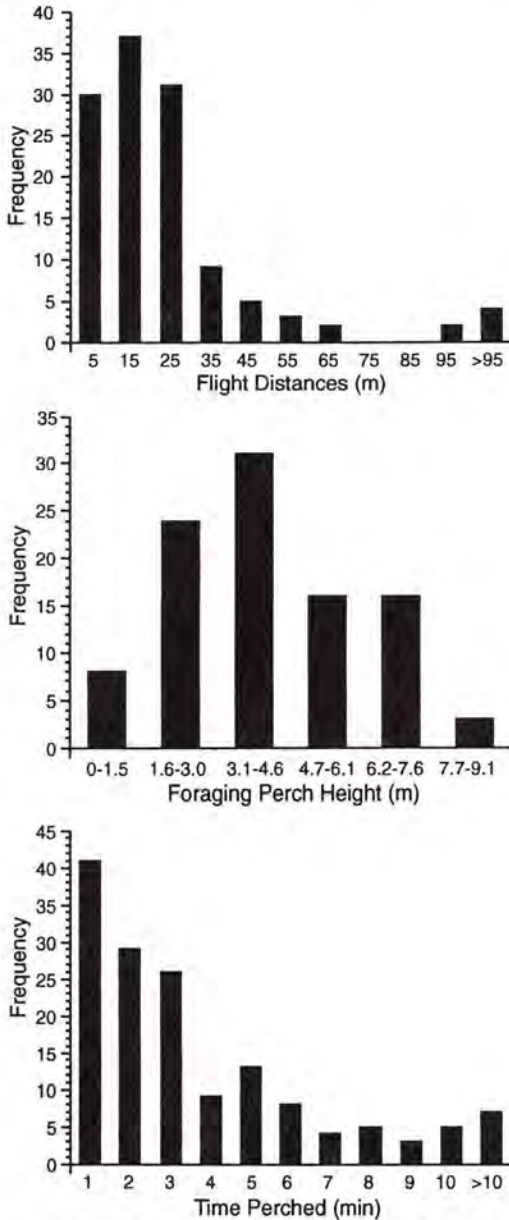


Fig. 4. Foraging behavior of boreal owls described by the distribution of flight distances, perch heights, and duration of search times for owls recorded during 18 foraging bouts in Chamberlain Basin, Idaho.

roost locations for an individual as subsamples.

The distance between male owl daytime roosts and nests also provides some insight on the magnitude of daily movements.

Nesting males rarely roosted within 500 m of the nest, and over 85% of roosts were over 1,000 m from the nest (some up to 5,600 m away). The average roost-to-nest distance of 5 owls over the 4-year study was  $1,729 \pm 831$  m.

Night radiotelemetry (triangulation) indicated that the roost-to-nest distances were accurate estimates of foraging distances. Following prey deliveries at the nest, 1 owl on 3 nights returned to the area of its day roost several kilometers from the nest. Four other males also left the nest stand immediately after prey deliveries to forage in areas distant from the nest.

*Daily Movements and Foraging.*—Boreal owls can be classified as sit-and-wait predators or searchers (as opposed to pursuers), but are very active while hunting. During a foraging bout, the birds move through the forest in an irregular or zigzag pattern, flying short distances between perches (Hayward 1987). They spend a majority of time perched; little time is spent actively pursuing prey. While perched, the owl constantly looks about with rapid head movements, apparently responding to forest sounds. We distinguished hunting activity from roosting by the rapid, jerking head movements of the bird and the bird's intense, wide-eyed appearance.

To quantify the strategy employed by boreal owls during foraging, we recorded flight distance between perches, time spent on each perch, and perch height during diurnal and nocturnal foraging bouts (Fig. 4). We observed hunting owls on 16 nights and recorded quantitative data on 10 occasions for 5 owls. These observations spanned 31.25 hours. After dark, the owl often was seen only intermittently despite our use of night vision goggles and beta-lights (Hayward 1987). We watched owls hunt during daytime 13 times and recorded quantitative results on 8 days for 4 owls. All quantitative results refer to foraging during summer (snow-free conditions) although we did pursue foraging birds in winter.

Owls flew an average of  $25 \pm 8$  m between hunting perches in 123 recorded

flight distances for 8 owls. The median distance between perches was 17 m, and over 90% of recorded flights were estimated to be <40 m (Fig. 4). In the forest environment we were unable to record long flights; therefore, our sample has a negative bias. We feel this bias influenced the observations only slightly. Over 75% of all flights were 25 m or less. Most often when we lost contact with an owl, the radio signal suggested that the bird made several flights with only brief perching periods.

Although the pattern of foraging flights varied, the owls often concentrated their activity in a relatively small area compared to the total length of all flights in a foraging bout. The owls we followed doubled back frequently and thus covered a relatively small area within several forest stands rather than a long narrow path.

While searching for prey, boreal owls perch on low branches. Perches during foraging observations averaged  $4 \pm 0.6$  m high ( $n = 114$ ). Seventy-five percent of 114 perches were <5.5 m and ranged from 0.5 to 9 m (Fig. 4).

Boreal owls search briefly from each hunting perch, but, as shown above, hunt a forest stand intensively by moving short distances between perches. We measured the duration of 150 hunting perches during 18 foraging bouts of 8 owls. Over 78% of perches were occupied <5 minutes, 64% for <3 minutes, and 27% for 1 minute or less (Fig. 4). Four percent of hunting perches were used >10 minutes. If an owl used a perch for >10 minutes, it either ceased foraging or was intently listening to a potential prey. One owl, observed hunting at night, watched a tight clump of branches in a lodgepole for 12 minutes prior to flying 2 m to attack a roosting passerine. Another owl, hunting during daylight, flew approximately 4 m to catch a southern red-backed vole (*Clethrionomys gapperi*) deep in a clump of common beargrass (*Xerophyllum tenax*) after watching the spot for 10 minutes.

*Seasonal Movements.*—Boreal owl activity shifted in elevation between summer and winter, but the change in activity did not involve a complete shift in home range.

Each of 12 owls radio marked during both winter and summer used summer roost sites with a higher average elevation. The difference in average seasonal roost elevation was  $186 \pm 105$  m ( $n = 12$ ). Three owls (2 males and a female) used roosts during summer that averaged over 335 m higher than winter roosts.

Although the owls demonstrated a consistent tendency to concentrate use at higher elevations in summer, the range of elevations used in winter and summer overlapped completely. During winter, owls spent some time in the highest portions of the study area despite snow depths over 2 m. Likewise, in summer, owls roosted on some occasions in the lowest portion of their home range. The major difference in seasonal use was the proportion of time that birds spent in each elevation zone.

Female movements after the brooding period (nestling age of 20–26 days) were variable. During incubation and brooding, 8 radio-marked females were never found over 200 m from the nest tree. When the young reached 20–26 days old, females ceased occupying the cavity. We monitored 6 radio-marked females immediately following the brooding period. In 2 cases, females left the study area within 3 days of leaving the nest cavity. In both cases, the young fledged successfully. In 2 cases, females occupied the home ranges used prior to nesting and assisted in feeding the young at the cavity and after fledging. One female assisted feeding young at the nest and remained within 3 km of the nest for 2 weeks. She then moved 17 km within 3 days and settled in an area of <400 ha that she occupied for at least the next 2 months. In a final case, the nesting male abandoned the nest 1–3 days prior to the normal date for the female to leave the nest. She left the nest 1 day later on 10 July. Marks on an event recorder at the nest and fresh prey in the cavity on 15 and 19 July suggested that the female fed the young on 2 nights. By 22 July, however, she began using an area 4.5 km from the nest where she remained for 2 months.

*Year-to-year Movements.*—Movements of radio-marked owls provide some indi-



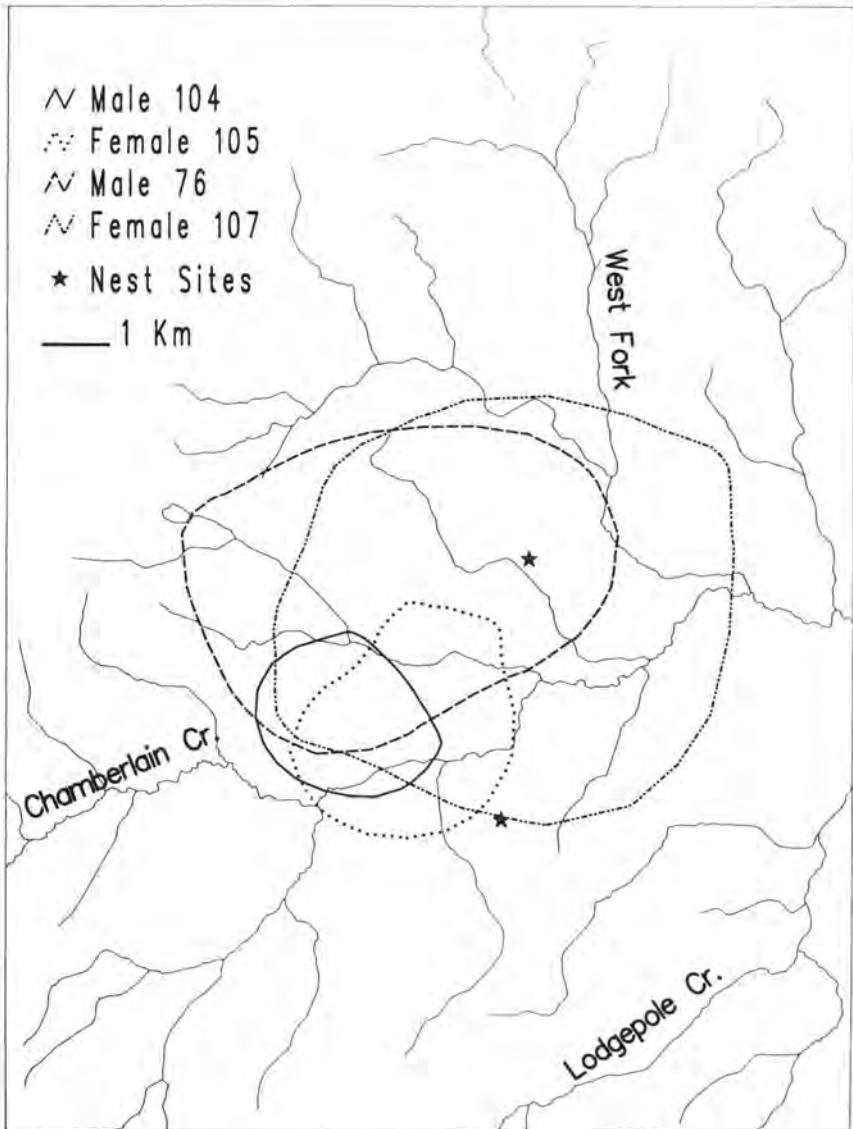


Fig. 5. Seasonal 95% utilization distributions of 4 boreal owls based on daytime roost locations in Chamberlain Basin, Idaho, during winter 1987. Owls 104 and 105 nested at the southern (lower on figure) site, and owls 76 and 107 initiated a nest at the northern site.

cation of the degree of site tenacity in the RNRW. We gathered evidence suggesting boreal owls in RNRW exhibit both year-to-year site tenacity and nomadic emigration. In late summer or autumn 1984-87, we placed new radio transmitters on 4, 5, 2, and 5 owls, respectively, in an effort to relocate the birds the following winter (4 months later). We observed male and female boreal owls who stayed in the basin for >1 year and used the same home range.

We also documented emigration of adults from the population.

Using evidence from both radio-marked birds and banded individuals, we found 6 males and 4 females that remained in the basin for >1 year. The 6 radio-marked males each used portions of their original home range in the second year. For 2 males monitored through both winter and summer in 2 years ( $\geq 20$  locations/season), seasonal home ranges from the 2 years

Table 12. Seasonal home range size (ha) for boreal owls in Chamberlain Basin, Idaho, during 1984–87. Areas are 95% utilization distributions calculated using the harmonic mean method (Samuel *et al.* 1985).

Year	Owl	Sex	Home range area					
			Winter		Summer		Combined	
			Size	No. of locations	Size	No. of locations	Size	No. of locations
1984	33	M					814	13
	34	F	320	10			607	20
	37	F	1,504	16			4,127	24
	42	M			610	16	1,166	24
1985	43	M	1,411	19	530	14	2,341	33
	76	M	1,282	24	229	19	2,581	43
	77	M	2,359	31	1,265	14	2,360	45
	84	M	946	12	1,421	17	2,141	29
1986	95	F	1,832	12				
	96	M			1,100	53	1,438	58
	97	M	2,001	13	2,386	27	6,876	40
1987	55	F			1,448	40		
	96	M	261	21	797	37	911	58
	76	M	2,259	28	1,520	45	1,761	73
	104	M	473	22	884	38	1,019	60
	105	F	826	17	747	21	1,122	38
	107	F	3,390	30	2,037	17	3,517	47
	117	M			1,884	20	1,161	26
133	F			874	18			

matched closely. One of the males nested in cavities 1.3 km apart in consecutive years. Home range information was not as complete for the 4 females that were radio marked for more than 1 year; however, all 4 remained within the Chamberlain study area.

Each year we checked most nest cavities used by owls in previous years ( $n = 23$ ). Although 2 nest trees were reoccupied, we never located an individual female in the same cavity she used previously. Nest sites of 2 individuals were known for 2 years. One female nested with different mates in 1984 and 1986 in cavities 1.4 km apart. The second female used cavities 7.6 km apart in 1987 and 1988.

In view of the evidence for year-round residency, several observations of emigration are important. As presented earlier, 2 females emigrated immediately after nesting and a third moved 17 km 2 weeks after nesting. We also witnessed the emigration of 2 males during a 2-week period in early February 1986. During the same 2-week period, another male died (1986 marked the low point in breeding effort and breeding success during the study). Both emi-

grating males wore new radio transmitters. Neither owl was relocated in the study area during repeated ground and air searches that winter. One of the males, first captured in February 1985 and monitored until February 1986, was relocated on 7 May 1986 near Upper Payette Lake, Valley County, Idaho, 80 km to the west of its former home range. The other male, first captured in February 1984, was monitored moving south from its home range and left the basin after living there at least 2 years.

*Home Range Area.*—We estimated the area used by boreal owls at Chamberlain during winter and summer from radio-marked owls in 1984–87 (Fig. 5). Mean winter home ranges averaged  $1,451 \pm 552$  ha (adaptive kernel estimate  $2,487 \pm 1,218$  ha) for 13 owls (5 females, 8 males) over the 4-year study. Summer ranges generally covered smaller areas; they averaged  $1,182 \pm 335$  ha (adaptive kernel estimate  $2,269 \pm 1,644$  ha) for 15 owls (4 females, 11 males). Year-round ranges averaged  $2,048 \pm 818$  ha (adaptive kernel estimate  $3,750 \pm 1,645$  ha) for 17 owls (4 females, 12 males) (Table 12). These values must be considered minimum home ranges. Our

Table 13. Diet of boreal owls at Chamberlain Basin, Idaho, estimated from pellets, cached prey, and nest contents of 31 owls in 1981 and 1984-88.

	Percent of prey items						Year-round	
	Winter			Summer			% of prey items	Biomass <sup>a</sup> (%)
	Male	Female	Total	Male	Female	Total		
Mammals								
Southern red-backed vole ( <i>Clethrionomys gapperi</i> )	49	49	49	34	13	31	36	37
Northern pocket gopher ( <i>Thomomys talpoides</i> )	8	6	7	10	16	11	10	26
Unidentified shrews ( <i>Sorex</i> spp.)	15	6	12	11	10	11	11	3
Unidentified voles ( <i>Microtus</i> spp.)	12	7	11	8	12	8	9	11
Deer mouse ( <i>Peromyscus maniculatus</i> )	6	10	7	5	5	5	6	5
Heather vole ( <i>Phenacomys intermedius</i> )	2	0	2	5	2	4	4	3
Northern flying squirrel ( <i>Glaucomys sabrinus</i> )	1	14	5	0	tr <sup>b</sup>	tr	1	7
Yellow-pine chipmunk ( <i>Tamias amoenus</i> )	2	0	1	2	2	2	2	3
Western jumping mouse ( <i>Zapus princeps</i> )	0	0	0	3	0	2	2	1
Pika ( <i>Ochotona princeps</i> )	0	0	0	tr	1	tr	tr	tr
Bushy-tailed woodrat ( <i>Neotoma cinerea</i> )	0	0	0	0	1	tr	tr	tr
Unidentified weasel ( <i>Mustela</i> spp.)	0	1	tr	0	0	0	tr	tr
Water vole ( <i>Microtus richardsoni</i> )	0	0	tr	0	tr	tr	tr	tr
Birds	4	6	5	6	1	5	5	3
Insects	1	0	1	16	37	18	13	1
Total count	144	69	242	572	93	672	914	26,162

<sup>a</sup> Biomass calculated using values in Table 14.<sup>b</sup> tr indicates <1%.

Table 14. Mean mass of small mammals used to calculate biomass of prey consumed by boreal owls. Measurements from individuals trapped in Chamberlain Basin, Idaho, 1984-87, except northern pocket gopher and northern flying squirrel values from Hall (1946).

Species	Age	Mass (g)	±95% CL	Sample size
Southern red-backed vole	Adult	26.5	0.74	100
Southern red-backed vole	Juvenile	12.2	0.67	48
Deer mouse	Adult	24.2	1.15	32
Deer mouse	Juvenile	11.5	2.16	6
Heather vole	Adult	22.7	3.47	9
Heather vole	Juvenile	13.8	5.01	3
Unidentified voles	Adult	30.0	3.01	12
Unidentified voles	Juvenile	12.2	2.11	9
Unidentified shrews		6.10	0.58	18
Western jumping mouse	Adult	20.81	2.57	14
Yellow-pine chipmunk		50.8	2.30	24
Northern pocket gopher		101.2		
Northern flying squirrel		140		



sample of each owl's activity was small, and (similar to other kernel estimators) the harmonic mean is biased low with small samples. Home range estimates, however, did not increase with sample size (see Hayward et al. 1987b for further discussion of seasonal home range use).

*Home Range Overlap.*—Our observations indicated that boreal owls did not use exclusive home ranges. Home ranges overlapped considerably, regardless of owl sex (e.g., Fig. 5). All of the owls we monitored in Ranch Creek or Flossie Creek drainages (where our sample was largest,  $n = 13$ ) had a home range that overlapped some other monitored owl by  $>50\%$ . Because they are most likely to defend a nesting territory, overlap of male home ranges is of greater interest (Lundberg 1979). In any year, male owls inhabiting the same drainage used the same forest stands intensively. During winter, when males establish small nesting territories (Mikkola 1983), distances between harmonic mean centers of activity (Samuel et al. 1985) were as low as 840 m. During summer, harmonic mean centers of activity were as close as 1,450 m, and neighboring nest sites were within 700 m. We found males roosting within 200 m of one another in both winter and summer. On 2 nights we captured 2 and 3 males at a single trapping site indicating common use of the site.

### Food Habits

Boreal owls at Chamberlain killed a wide range of prey including small mammals, small birds, and insects (Table 13). The list of small mammals in the diet includes all species of mammals smaller than 50 g known to inhabit the basin except the water shrew (*Sorex palustris*). Because of incomplete skulls, bones of several large shrews found in pellets could not be identified, but were probably water shrews. Avian prey included 7 passerines and 1 Piciformes (Hayward 1989:46). Crickets numerically dominated insect remains.

The breadth of species represented in owls' diets contrasted with the narrow range of prey taken frequently. Small

mammals accounted for 79.4% of 914 prey identified and over 95% of the biomass estimated from pellets and nest sites of 32 owls (Tables 13, 14). Southern red-backed voles and pocket gophers together accounted for over 63% of estimated prey biomass, underscoring the limited number of prey species important to the owls. Southern red-backed voles alone accounted for 36% of individual prey in our sample from winter and summer.

Diets of individual male owls differed significantly in both winter and summer (summer  $\chi^2 = 55$ ,  $df = 25$ ,  $P < 0.01$ ; winter  $\chi^2 = 20$ ,  $df = 10$ ,  $P = 0.025$ ). In our test of heterogeneity among individuals, we considered only those owls for whom we recorded 30 or more prey items in 1 season (6 males in summer, 3 males and 1 female in winter). We eliminated the single female from the winter sample because we wished to determine whether individuals of the same sex fed similarly within a season. In these tests we included only the 5 most common small mammal prey.

Major differences in diet among individuals involved unusual numbers of uncommon prey taken by particular owls. Although samples from some boreal owls included no avian prey, the diet of 1 male included 10% birds during summer (41% of all avian prey taken by 8 males during summer). This same male captured 54% of the chipmunks (*Tamias amoenus*) taken by males during summer. Two other individuals captured many western jumping mice (*Zapus princeps*) and crickets. Despite these differences, southern red-backed voles were the most frequent prey for all individuals in both winter and summer.

*Seasonal Prey Use.*—During winter, owls relied on southern red-backed voles for nearly 50% of prey (Table 13). The number of prey taxa available in winter is less than in summer and is reflected in fewer species in the winter diet. Northern pocket gophers (1 of the most frequent summer prey), western jumping mice, and yellow-pine chipmunks are all unavailable during the period of winter snow pack. (During early and late winter when snow

Table 15. Frequency of capture for 7 species of small mammal in 9 × 10 snap-trapping grids at 7 sites in Chamberlain Basin, Idaho, during 1984–87. Trap sites are labeled by dominant overstory vegetation. Each grid was run for 7 days during late May or early June for the number of years listed.

Small mammal species	Sage (4 yrs)		Wet meadow (3 yrs)		Lodgepole 1 <sup>a</sup> (4 yrs)		Lodgepole 2 <sup>b</sup> (3 yrs)		Douglas-fir (4 yrs)		Mixed conifer (5 yrs)		Spruce-fir (2 yrs)	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Southern red-backed vole	0	0	0	0	0	0	1	0	12	0	9	2	66	38
Deer mouse	3	0	0	0	3	0	1	0	7	1	7	3	0	0
Unidentified shrews <sup>c</sup>	0	0	16	0	4	0	1	0	0	0	1	0	0	71
Unidentified voles	7	2	5	0	0	0	0	0	0	0	0	0	0	0
Western jumping mouse	2	0	1	0	8	0	0	0	0	0	3	0	0	0
Heather vole	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Yellow-pine chipmunk	18	0	1	0	3	0	4	0	1	0	4	0	0	0

<sup>a</sup> Lodgepole-pine forest with lush understorey vegetation and some downed logs.

<sup>b</sup> Lodgepole-pine forest with dry understorey and no downed logs.

<sup>c</sup> Shrews were not aged.

cover is patchy, these species are captured and, therefore, are reported in the winter diet.) In spring, the earliest recorded dates for chipmunks or jumping mice in pellets or nest material were 14 March and 22 May, respectively. Pocket gophers were recorded in pellets by 15 March. Once available, pocket gophers were taken often and accounted for 15% of overall winter prey biomass (7% by frequency) despite the limited period they were available. Based on skeletal measurements (Janes and Barss 1985) of a sample of pocket gopher remains in pellets ( $n = 17$ ), 41% of pocket gophers captured were 30 days old or younger.

Flying squirrels were the only prey taken much more often in winter than summer. Of 12 recorded flying squirrels, 11 were captured during winter, 10 of these by females. The squirrels represented 45% of prey biomass recorded for female owls during winter, indicating the importance of these prey during a period when other prey are less available.

During summer, southern red-backed voles continued to be the most frequent prey and accounted for 29% of biomass consumed. The owl summer diet was diverse compared to winter with the addition of chipmunks, jumping mice, and crickets. Crickets may be more important to owls than our sample suggests. We rarely found crickets during searches at nests for prey, but photographs of prey deliveries showed several crickets. Also, pellets composed largely of insects break apart more quickly and, therefore, are less likely to be found at roosts.

*Yearly Variation.*—The frequency of southern red-backed voles in prey samples was lower in 1986 (the year of poor owl breeding) than in other years. In 1986, 26% of prey were southern red-backed voles compared to 38, 44, and 45% in 1984, 1985, and 1987, respectively. As a result, deer mice (*Peromyscus maniculatus*), pocket gophers, and heather voles (*Phenacomys intermedius*) increased in pellets in 1986 compared with other years. The frequency of *Microtus* spp. remained relatively constant from 1984 to 1987 and averaged 11%. The frequency of the other common prey,

Table 16. Frequency of capture for small mammals in pit traps set year-round at Chamberlain Basin, Idaho, during 1984–87 in 7 vegetation types defined by dominant overstory. Three sites were trapped for each vegetation type except spruce bottom, where only 2 sites were trapped. Trap days in thousands are recorded in parentheses.

Small mammal species	Sage (2.9)	Wet meadow (2.8)	Lodgepole (3.3)	Mixed conifer (3.3)	Douglas- fir (3.0)	Spruce bottom (2.3)	Spruce- fir (2.4)
Southern red-backed vole	0	0	9	5	25	32	52
Unidentified shrews	25	45	19	28	16	77	45
Deer mouse	11	0	5	10	2	5	3
Unidentified voles	23	5	0	0	0	0	0
Western jumping mouse	4	1	1	0	0	1	0
Heather vole	0	0	2	1	0	0	3
Yellow-pine chipmunk	6	0	9	18	6	0	0
Northern pocket gopher	4	3	5	0	1	0	1

shrews, and birds also remained relatively constant.

*Small Mammal Habitat Use—Comparison of Sampling Methods.*—Because small mammals accounted for 80% of the boreal owl diet at Chamberlain, we used snap and pit trapping to determine habitat associations of small mammals (Tables 15, 16). Neither method can give a completely accurate ranking of species abundance within various habitats. By using both methods we sought to sample a broad range of mammal species and rank the importance of various vegetation types for each prey species.

Southern red-backed voles, shrews, and deer mice were the most frequently captured species by both methods (Tables 15, 16). To compare the 2 trapping methods, we examined capture rates for these 3 small mammals across 6 vegetation types using the 2 trapping methods. Capture rates of southern red-backed voles in pit and snap traps were strongly related (Spearman rank correlation,  $r_s = 0.94$ ). The 2 trapping methods also resulted in similar ranking for shrew abundance ( $r_s = 0.75$ ). Capture rate for deer mice differed ( $r_s < 0.10$ ) mainly because pit traps in Douglas-fir forests captured few mice, whereas the number of snap-trapped mice was highest for this habitat. Otherwise the rank order of the habitats was similar for snap- and pit-trap samples of deer mice.

An important difference in pit-trap and snap-trap samples was the frequency of pocket gophers in the pit-trap sample (Tables 15, 16). Pit traps captured pocket go-

phers on 5 sites, whereas snap traps did not capture gophers.

*Vegetation Association of Small Mammals.*—Southern red-backed voles were captured in both pit and snap traps more frequently in spruce-fir forest than other types (Tables 15, 16). Average pit-trap capture rates across all years and sites were 2.4 times greater in upland spruce-fir than other types. Snap trapping indicated even larger differences in vole abundance between spruce-fir and other types. Average capture rates in spruce-fir exceeded all other forests by an order of magnitude. Southern red-backed voles occurred in all forest vegetation types but capture rates were low in lodgepole-pine and dry mixed-conifer forests. In both spruce-fir and Douglas-fir forests the biomass of southern red-backed vole captures exceeded that of other small mammals. We did not capture southern red-backed voles on nonforested sites.

We combined *Sorex vagrans* and *S. cinereus* for discussion of distribution and abundance. We captured shrews at all pit-trap sites, and variation in capture rates among habitats was lower for shrews than other small mammals (Table 16). Shrews were captured by both trapping methods most frequently in spruce-fir forests, including both spruce bottoms and upland spruce-fir forests. Using pit traps, more shrews than other mammals were captured in lodgepole-pine, mixed-conifer, and unforested habitats.

We captured deer mice in all vegetation types except wet meadow. Pit- and snap-



Table 17. Trend in boreal owl populations at Chamberlain Basin, Idaho, during 1984–87.

Survey effort and results	Survey period			
	1984 18 Jan–23 Apr	1985 <sup>a</sup> 25 Jan–2 May	1986 14 Jan–7 May	1987 16 Feb–27 Apr
No. surveys	13	29	32	36
No. listening nights	5	16	5	19
Kilometers surveyed	64	195	217	218
% surveying or trapping nights males heard	56	51	8	49
% surveying nights calling males heard	62	48	6	53
No. calling males heard per survey km	0.24	0.07	0.02	0.14
No. owls captured				
winter	9	5	3	7
year	9	6	4	8

<sup>a</sup> Four people worked in 1985 and 1987; 2 people in 1984 and 1986.

trap results, however, differed in the rank order of deer mice captures across habitats. In pit-trap samples, deer mice were most frequently captured in sagebrush–bunchgrass habitats where they were the most frequently captured mammal. Deer mice also were captured often in mixed conifer by pit traps, but rarely in Douglas-fir. Snap-trapping results showed Douglas-fir as the most important habitat for deer mice followed by mixed conifer, lodgepole, and sagebrush–bunchgrass. During 2 years of snap trapping in the spruce–fir grid, no deer mice were captured.

We found chipmunks in all habitats except spruce–fir bottoms and spruce–fir uplands. Capture rates were the highest in the drier habitats—sagebrush–bunchgrass (snap trapping) and mixed conifer (pit trapping).

Montane voles (*Microtus montanus*) and long-tailed voles (*M. longicaudus*) used narrower ranges of habitat than other common small mammal species. Using both the pit and the snap traps, we caught *Microtus* spp. only in nonforested habitats. *Microtus* capture rates were higher at sagebrush–bunchgrass sites than in wet meadow.

Pocket gophers, jumping mice, and heather voles were caught in several habitats, but less frequently than the species discussed above. Dirt mounds and “soil ropes” seen throughout the study area suggested that pocket gophers used all but the most rocky habitats. Pit-trap capture rates of pocket gophers were highest in sage-

brush–bunchgrass and lodgepole habitats. Jumping mice were found in a variety of forested and nonforested habitats, but were never captured at our Douglas-fir or spruce–fir sites (Table 16). Heather voles were rarely captured (8 individuals in pit and snap traps combined), yet they were found in all forest vegetation types. These voles did not occur in any of the nonforested types.

The water shrew was captured with a pit trap on a single site in a wet meadow. This site was inundated for several weeks each spring.

### Owl Population Characteristics

*Yearly Variation in Owl Abundance.*—During the study, we recorded data that may be used to form several crude indices to breeding abundance and breeding productivity each year. Together these measures provide evidence of the minimum number of breeding owls and year-to-year changes in breeding effort or productivity at Chamberlain and Cold Meadows. Each of the indices discussed below is untested and, therefore, has unknown bias.

Nighttime surveys using playback of taped boreal owl calls during each winter show the yearly variation in breeding population abundance from 1984 to 1987 at Chamberlain and 1984 to 1986 at Cold Meadows (Tables 17, 18). At Chamberlain, 2 related indices show a slight decline in 1985 followed by a substantial decrease in breeding activity in 1986. The proportion

Table 18. Trend in boreal owl populations at Cold Meadows, Idaho, during 1984–86.

Survey effort and results	Survey periods		
	1984 19 Feb–4 Mar 3 Apr–11 Apr	1985 25 Feb–7 Mar 6 Apr–18 Apr	1986 27 Mar–11 Apr
No. surveys	17	20	11
Kilometers surveyed	74	100	70
% surveying nights calling males heard	40	20	18
No. calling males heard per survey km	0.20	0.07	0.09

of survey nights on which we heard boreal owls differed significantly among years ( $\chi^2 = 20.2$ ,  $df = 3$ ,  $P < 0.0001$ ). The low number of successful nights in 1986 contributed most to the difference (cell  $\chi^2 = 8.54$ ,  $P = 0.0035$ ). If instead, we look at the number of male owls heard singing per mile surveyed, the same pattern is apparent—owl calling rate dropped from a high in 1984 to a low in 1986 with a recovery in 1987 (Table 17). This result suggests that differences between years in the number of miles surveyed in a given night or the total number of survey nights was not responsible for the observed trend. Each year of the study some new routes were surveyed, which added to the total survey mileage. Routes surveyed in earlier years were always resurveyed.

Survey results at Cold Meadows showed a similar pattern. The proportion of survey nights that we heard boreal owls was twice as large in 1984 as in 1985 or 1986, but the difference was not significant ( $\chi^2 = 2.65$ ,  $df = 2$ ,  $P = 0.265$ ). The number of calling males heard per survey mile was higher in 1984 (Table 18) than in either of the following years.

The pattern of declining breeding populations of boreal owls from 1984 to 1986 before rebounding in 1987 also was reflected in our winter trapping success at Chamberlain. We captured 9 boreal owls in 1984, 5 in 1985, 3 in 1986, and 7 in 1987. Trapping effort for each year is difficult to quantify because our trapping strategy differed among years. The number of nights we trapped at sites where we had little confidence of capturing an owl differed among years. Using the number of trapping nights as an imperfect measure

of effort, catch per unit effort during winter equaled 1.8 for 1984, 0.29 for 1985, 0.60 for 1986, and 1.67 for 1987. Again, 1985 and 1986 showed the lowest values.

As a final index to breeding population trend at Chamberlain, we used a method similar to spot mapping. Our earlier indices using number of males heard per mile surveyed or per survey night included owls heard calling from the same site during different surveys. We sought to remove this bias by defining the number of male territories located each year by assigning singing males heard in 1 forest stand on different surveys to 1 territory. We found 12 territories in 1984, 14 in 1985, 3 in 1986, and 19 in 1987. During the study, the area surveyed increased each year. An imperfect way of standardizing the number of territories is to divide by the number of kilometers surveyed. Territories located per kilometer surveyed equaled 0.65 in 1984, 0.24 in 1985, 0.04 in 1986, and 0.26 in 1987.

*Yearly Variation in Productivity.*—Productivity at nest sites was not constant from year to year. At Chamberlain we located 3 nests in 1984, 2 in 1985, 3 in 1986, and 8 in 1987. The number found was related to the owl breeding effort, the number of radio-marked owls, and our experience locating nests. From this small sample, we observed the rate of nest abandonment, clutch size, and number of young fledged per nest that fledged young.

In all but 2 cases, we observed the clutch size during incubation or at hatching, so we can only estimate minimum clutch size. During 1984–87, boreal owl clutches ranged from 2 to 4 eggs and averaged 3.3, 2.5, 2.5, and 3.5 eggs for each year 1984–

87, respectively. Only 2 nests during this period fledged 3 young (1 nest in 1984 and 1 nest in 1987); for the remaining nests, those which fledged young each produced 2 owlets. Clutch size and fledging rate, then, both indicated that 1984 and 1987 were more productive than the intervening 2 years.

Although clutch size and the number of fledglings per successful nest were higher in 1984 and 1987, complete nest failure appeared to contribute most to variation in productivity. Nests failed due to parental abandonment, nest predation, and death of an adult. The pattern of nest failure across years appeared to follow the other measures of breeding activity (calling) and productivity. During 1984–87, nest histories included complete success of 3 nests in 1984, abandonment of 1 of 2 nests in 1985, loss of all 3 nests in 1986, and loss of 6 of 8 nests in 1987. The timing and reasons for nest failure each year is important in evaluating trends in productivity. In years when other measures of productivity were low (1985, 1986), 3 of 4 nests that failed were abandoned early in the nesting cycle. The other nest failed due to predation. In good years (1984, 1987) predation was responsible for all nests that were lost.

*Annual Survival.*—During 1984–88, we monitored 24 adult boreal owls from late January through August using radiotelemetry. Each autumn we placed a fresh radio on any marked birds in an effort to recover the birds the following January. Ten owls were followed during more than 1 year. Records from the radio-marked owls give some insight into mortality rates and emigration from the population.

Radio packages certainly increase energy expenditure of the owls and may increase risk of predation. The extent to which radio packages reduced survival of marked owls cannot be assessed with our data. The longevity we witnessed in several marked owls suggests that the impact was not severe. One male and 1 female wore radio tags for 916 and 824 days, respectively, and were still alive at the end of the monitoring period. More impor-

tantly, we weighed each marked owl upon initial capture and at each recapture. Average recapture weights exceeded initial capture weights for 4 of 7 individuals who were weighed on 4 or more occasions. For owls recaptured on fewer occasions, body mass showed no trend. These results suggest that the radio transmitters did not prevent the owls from maintaining normal body mass. Whether the owls were forced to actively forage for longer periods, exposing themselves to predation, cannot be addressed.

During the study, 6 owls (3 males and 3 females) died. Two owls that died during winter (a male and a female) appeared to have starved; they showed no sign of injury. The male who had been monitored for 201 days was found within hours of his death and had lost 23 g (20% of body weight) in 12 days. Three birds (2 females and a male) were consumed in part or entirely by predators. Another male died of unknown causes.

A minimum of 5 marked owls (2 males and 3 females) was lost from the population through emigration. In 3 cases, we monitored the owls as they left the basin; 1 was relocated 80 km west, near Upper Payette Lake, Valley County, Idaho. Behavior prior to loss of contact led us to conclude that 2 other owls also emigrated.

We used information from the radio-marked owls to estimate survival of adult boreal owls (Heisey and Fuller 1985). Our analysis assumes that adult male and female boreal owls experience equal survival and that survival rate during any given year can be treated as constant throughout the year but that survival may differ between years. Because of relatively small samples within any year, estimates of yearly survival include extreme confidence intervals; therefore, we consider estimates for the entire study period only.

Because we monitored owls from mid-winter through summer in most years, estimates of survival restricted to this period are most legitimate. Our analysis, then, treats only the fate of owls during this monitoring period. For instance, an owl that was remarked in autumn but could



not be located the next year was not considered a loss because it survived during the monitoring period. If an owl was observed emigrating from the area, it was included in the analysis as described below.

It could be argued that owls who emigrate are rarely recruited to a new population. If we assume that all birds that emigrated during the monitoring period died and that no adult owls successfully immigrated into the population, then all emigration can be treated as a loss from the adult breeding population. These assumptions provide a conservative estimate of survival for adult, radio-marked owls during our investigation. Under these assumptions, finite survival from midwinter through summer, expressed as a yearly rate, averaged 20% (95% CI = 7–55%).

A liberal estimate of survival for adults in the owl population could be formed by assuming that all emigrating owls survived and that immigration into the population equals the emigration we observed. Under this assumption, only direct mortality is considered a loss. Finite survival from midwinter through summer expressed as a yearly rate averaged 46% (95% CI = 23–91%).

*Breeding Chronology: Courtship.*—At Chamberlain, male boreal owls began courtship singing by late January in most years. In 1984 and 1985, we began surveys during the last week of January and heard owls on the first or second night in both cases. The calling rate, measured as the number of owls heard per survey night, increased from January through March.

Female owls were observed at male calling sites early in the courtship period. On 5 February 1984, we captured a female at a calling site while a male called 10 m away. The same year, we heard a male and female together on 7 February. In 1987, we heard both members of a mated pair on 16 February (our first night surveying the route) and captured both owls on 20 February. The owls repeatedly visited the site to court throughout the winter and began nesting 20 April in a snag about 40 m from the capture site. In 1986 both

members of a pair were heard calling at a nest cavity 2 months prior to egg laying.

Throughout courtship, the birds associated with one another mainly during nighttime rendezvous at the potential nest site; members of radio-marked, mated pairs rarely roosted together during daytime. Our observations suggest that pairs do not rendezvous at the nest every night during courtship (Hayward 1989:56–57). On nights when the owls do rendezvous, they meet at any time through the night rather than consistently meeting shortly after sundown.

Our observations suggest that at night, during the courtship period, male boreal owls sing most often within 150 m of a selected nest cavity, an exception being unmated owls early in the courtship period. During observations at nests of 4 radio-marked males on 14 nights prior to egg laying, the males never called farther than 150 m from the nest site. Usually the male sang from a tree adjacent to the nest tree or from inside the nest cavity. Because we were not following these males during foraging, however, these observations were not sufficient to determine if the males were singing at sites out of our hearing range. Other observations do suggest that early in the courtship period unmated owls call from several widely dispersed locations and that males visit stands where other males are singing. Even these dispersed singing locations were later determined to be sites used by boreal owls for nesting sometime during the study. On 14 February 1984, we captured 3 males while we played the boreal owl song at 1 site. One of the owls nested at the capture site that year, and 1 of the others moved about 6 km before the nesting season. On 18 February 1985, we captured 2 males when we played the courtship call at 1 site. One of these owls (BO77) nested in a stand 1.6 km from the capture site, and the other did not breed. The capture site had been used for nesting the previous year by a different male. Finally, on 31 March 1985, a male (BO84) was captured and radio tagged in the stand used by BO77 for nesting that year. BO84 was heard calling in the stand

Table 19. Nesting chronology of boreal owls at Chamberlain Basin, Idaho. In most cases laying date is estimated by aging nestlings found 1–4 days after hatching. We assumed in all cases that incubation lasted 29 days (Korpimäki 1981). First visit refers to the first time we observed eggs or young at the nest.

Year	Owl	Occupancy	Laying date	Hatching date	Fledging date	Female off	First visit
1984	34		17 May	15 Jun	7–12 Jul		Youngest 1 day old
	55		14 May	14 Jun <sup>a</sup>	15 Jul	4–6 Jul	Third egg laid
	58	18 Apr	7 May	5 Jun	2–8 Jul	22–26 Jul	Youngest 1 day old
1985	86	23 Apr	15 May	13 Jun	15 Jul	5 Jul	Youngest 1 day old
	87		20 May	18 Jun			Youngest 2 day old
1986	95	18 Apr	by 30 Apr <sup>b</sup>				
	55		24 May	22 Jun			During laying
1987	105	13–14 Apr	21 Apr	20 May	16–18 Jun	9 Jun	Youngest 2 days old
	107	16 Apr <sup>c</sup>					
	107	26–30 Apr	1 May	29 May			Youngest 4 days old
	115		12 Apr	11 May			Youngest 12 days old
	128	16 Apr <sup>d</sup>					
	133		17 Apr	16 May	14–15 Jun	6 Jun	Youngest 6 days old
1988	134		14 Apr	13 May			Unhatched egg
	135		17 Apr	18 May			Two unhatched eggs

<sup>a</sup> The date the third egg was laid and the date the first egg hatched were both known for this nest. The female had abandoned the nest for 2 days (between the second and third egg), which likely accounts for the long incubation period.

<sup>b</sup> Female abandoned the nest on 30 April without being disturbed, and 2 eggs had been laid.

<sup>c</sup> Female abandoned her first nest due to disturbance and initiated a second nest by 30 April.

<sup>d</sup> Female was killed by a predator away from the nest before laying.

on 7 April, but he failed to breed that year. On 24 March, when we played a tape-recorded boreal owl song at a calling site, 4 radio-marked owls, including the pair that nested at that site, moved to the stand.

**Breeding Chronology: Nesting.**—The end of courtship and beginning of nesting is not well defined because female boreal owls begin occupying the nest cavity prior to egg laying. We observed both the onset of nest occupancy and egg laying dates for 3 female owls. These birds began roosting in the nest cavity 10, 19, and 22 days prior to egg laying (Table 19). Early in this period, the female may spend some time away from the cavity foraging at night. Also the female may occupy the cavity intermittently. In 1987, a female occupied the cavity every other day for the first week of nest occupancy before spending consecutive days on the nest. On the other hand, in 1984, another female began roosting in the nest cavity on 18 April and appeared to occupy the site continuously for 16 days before egg laying. The use of the nest cavity for roosting demonstrates an important change in behavior associated with nesting. Other than female owls oc-

cupying cavities during nesting, we never found a boreal owl roosting in a cavity in 882 roost locations.

Females consistently occupied the nest cavity in mid-to-late April (Table 19). Six recorded occupancy dates over 4 years ranged from 13 to 23 April. In 1987, 1 bird laid eggs by 12 April indicating an earlier occupancy date. Recorded laying dates ranged from 12 April to 24 May. Although our sample is extremely small, there is some suggestion that laying dates are rather consistent within years and vary more between years (Table 19). A majority of our data on laying dates came from radio-marked birds, so we know these observations do not represent renesting dates.

Females occupy the nest cavity day and night through incubation and most of the nestling period. We recorded the date when females ceased occupying the nest cavity with their young for 5 owls over 4 years. Four of these owls raised 2 nestlings each and left the nest when the oldest nestling was 20–22, 17–21, 22, and 20 days old. The other female raised 3 nestlings and left the cavity when the oldest was 21 days old. At 4 nests where we recorded

fledging dates, the oldest owlet fledged at 31, 32, 27–29, and 29–30 days old (Table 19).

## DISCUSSION

### Habitat Use

*Nesting Habitat.*—Our observation of nesting habitat demonstrated that boreal owls in the RNRW used sites that were not randomly chosen from among available habitats. Compared to available vegetation, breeding habitat use was concentrated in 2 types, mixed conifer and aspen. Forest structure at breeding sites also differed from the range of structures available. Furthermore, although not conclusive, a nest-box experiment implied avoidance of potential nest sites in lodgepole-pine stands when cavities were available elsewhere.

Boreal owl breeding habitat has not been studied quantitatively in Europe. Qualitative descriptions, however, include a wide range of habitats. In Germany, Jorlitschka (1988) noted breeding activity in old forest but not young forest. In Finland, Korpimäki (1981, 1988a) recorded nests in Norway spruce (*Picea abies*) and Scotch pine (*Pinus sylvestris*) forests, edges of bogs and lake shores, and in boxes on hay barns in mowed pastures. In Norway, boreal owls also nested in "areas dominated by cultivated land," bogland, and mixed Scotch pine and Norway spruce forest (Solheim 1983a:81). When suitable cavities are available (usually in artificial structures), boreal owls nest in forest clearcuts and forest with simple canopy structure (Sonerud 1986; H. Stein, Univ. of Oslo, Oslo, Norway, pers. commun.).

The relatively narrow range of breeding habitat use we observed contrasts with the variety of sites described in Europe. Several hypotheses could explain the differences in range of breeding sites used. Abundance and productivity differ between owl populations in Fennoscandia and the RNRW (Solheim 1983b, Korpimäki 1987c, this study). Theory (Fretwell

and Lucas 1969) and empirical results (e.g., Alatalo et al. 1985) suggest that the range of habitats used is related to population abundance. If owl populations are more dense in Fennoscandia, some individuals may be forced to use suboptimal breeding habitat (thereby expanding the range of sites used) especially in peak breeding years. Alternatively, breeding-site use may differ between Fennoscandia and the RNRW largely due to the distribution of available cavities among habitats. In Fennoscandian study sites, a majority of boreal owls nest in artificial structures and biologists note the paucity of natural cavities (Korpimäki 1981, Lofgren et al. 1986). The distribution of available nest sites is largely dictated by human placement of nest structures, and, in peak years, over 40% of available nest boxes may be used (Lofgren et al. 1986). Therefore, in Fennoscandia, nest-site use likely reflects nest-site availability rather than preference. In the RNRW, our nest-box experiment suggested that nest cavities were not limited. Use of a restricted range of vegetation conditions for breeding, then, may reflect preference; however, the availability of cavities was not the same across sites, and vegetation types with numerous cavities were used most frequently. Finally, compared to Europe, few breeding sites have been located in the northern Rockies. Therefore, sampling considerations alone could explain the differences.

We speculate that the consistent use of mature forest for breeding in the RNRW does not result from preference for mature forest structure *per se*. Rather, the owls may key on forests with this structure when searching for cavities because the probability of encountering suitable nest cavities is highest in forest with this structure. Mature and older conifer forest and aspen stands both have high densities of large diameter cavities. We believe the density of suitable cavities was much lower in other forest vegetation types. Although we did not measure cavity density, based on our observations during 4 years of field work, we believe density of large cavities may



be nearly 2 orders of magnitude greater in mixed-conifer and aspen forests (the vegetation types used for nesting) than in lodgepole or spruce-fir forests.

The mixed-conifer forest and aspen stands used by boreal owls at Chamberlain were unique forest sites. Both occurred in relatively small stands within the extensive lodgepole-pine, Douglas-fir, and spruce-fir forests. The occurrence of ponderosa pine within the subalpine-fir life zone is not common, and therefore the abundance of nest sites at Chamberlain may have been higher than is found in other areas of the northern Rockies. Aspen stands with large diameter individuals also are not common in the northern Rockies. At Chamberlain these stands generally occur on unique soil-topographic sites and exist as almost pure aspen.

*Roosting Habitat.*—Roost sites differed from breeding habitat and from paired random locations in the RNRW. Our observations showed that winter roosts differed only slightly from random sites, whereas the evidence for differences was greater for summer roosts. Site choice appears most critical in summer. Temperature measurements at roost sites and observations of owls gullar fluttering while roosting suggest that moderation of high summer temperatures may be an important function of summer roosts. We observed owls exhibiting gullar fluttering only during summer. On 2 occasions when we observed resting owls exhibiting gullar fluttering, the air temperature was only 18 and 23 C indicating that the birds can be heat stressed at moderate ambient temperatures.

Normal winter temperatures in the RNRW may not stress boreal owls, which are well adapted for cold (Mikkola 1983). The thermal neutral zone of the owl may encompass a majority of the temperatures experienced during winter in this region. Warm summer conditions, however, appeared to stress boreal owls. Behaviors to ameliorate warm conditions may involve roost stand selection.

Roost habitat characteristics have not been reported for European populations.

Palmer (1986) measured habitat at 174 roosts of 3 boreal owls in Colorado during 1 year. He noted a difference in roost characteristics and random sites but did not examine this pattern by season.

*Foraging Habitat.*—Our direct observations of foraging owls were insufficient to describe patterns of foraging habitat use. Observations of roost sites and food habits, however, provide empirical information that can be used to make inferences concerning foraging habitat use.

If roost sites represent the end of a foraging bout as we suspect from our observations of foraging owls, we may use our sample of roost locations as a preliminary sample of foraging sites. Data from 257 winter and 376 summer roost sites indicate frequent use of spruce-fir forests. In summer, 67% of all roosts were in spruce-fir forest and 26% in lodgepole. Winter roosts occurred in spruce-fir forest 35% of the time and in lodgepole forests 38% of the time. In both seasons, spruce-fir stands used by owls were usually mature or older forest sites. The frequent use of spruce-fir forest contrasts with the availability of spruce-fir in the area. Spruce-fir covers <10% of the study area, whereas lodgepole covers >50%.

Owl food habits and data on habitat use by small mammals support the contention that spruce-fir forest is important foraging habitat. During both winter and summer, southern red-backed voles were the most frequently captured prey (Table 13), especially in years when the owls bred most successfully. Spruce-fir forest supported the greatest number of southern red-backed voles and highest small mammal biomass. Southern red-backed voles were more abundant in spruce-fir forests than any other habitat we trapped. We captured 9 times as many southern red-backed voles in an old spruce-fir forest than we captured in any other vegetation type. Spruce-fir forests used by boreal owls in the RNRW were also generally old forest stands.

Palmer's (1986) observations of boreal owls in Colorado suggest that older spruce-fir forest is used for hunting. Studies in

Norway also have noted the importance of mature spruce forest for foraging (Sonerud 1986, Sonerud et al. 1986). Based on direct observations and composition of diet, the authors suggested that during winter and summer boreal owls foraged primarily in older forest sites. In early spring, immediately following snow melt, however, the owls hunted clearcuts. Sonerud (1986) speculated that the owls favored mature forest during winter because snow conditions (uncrusted snow) facilitated access to prey. In summer, mature forest sites had less herbaceous cover than open sites, which allowed greater access to prey. During the short period following spring thaw, before herbaceous vegetation became dense, the owls shifted to openings where densities of voles exceeded densities in forested stands.

### Home Range Area

Integrating our results concerning nesting, roosting, and foraging habitat use indicates that resources used by owls are not all provided by any single vegetation type. Because of the natural segregation of vegetation types in the landscape, habitat components used on a daily basis, especially in the courtship and breeding seasons, were dispersed geographically. Mixed conifer and stands used for nesting lie on the eastern side of the study area at lower elevations as do aspen stands that contain many potential nest cavities. Spruce-fir forests used for roosting and foraging, especially during summer, are concentrated at high elevations to the west. The geographic dispersion of habitats used for nesting, roosting, and foraging may be responsible, in part, for the large home ranges used by boreal owls in the RNRW.

The average winter and summer ranges for boreal owls compare with those cited by Lindstedt et al. (1986) for coyote (*Canis latrans*), red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), and American marten (*Martes americana*), all of which feed on similar prey. Among owls, our estimates of boreal owl ranges compare to, and in some cases exceed, those reported for larg-

er species. Thomas et al. (1990) reported median home ranges of spotted owls (*Strix occidentalis*) from studies in California, Oregon, and Washington that ranged from 571 to 4,021 ha; Forsman et al. (1984) reported home ranges <2,000 ha for spotted owls in Oregon; Hirons (1985a) reported Tawny owl (*Strix aluco*) territories <100 ha in England; Bull et al. (1988a) measured great gray owl (*Strix nebulosa*) home ranges that averaged 6,730 ha in Oregon; and Smith and Gilbert (1984) calculated home ranges for Eastern screech-owls (*Otus asio*) of under 150 ha. Boreal owl home ranges fell within the range reported for the largest owl, the eagle owl (*Bubo bubo*) of Europe (Mikkola 1983).

Several factors likely contribute to large boreal owl ranges. As noted above, no single vegetation type provides optimum nesting, roosting, and foraging habitat, and these vegetation types are geographically disjunct. Therefore, geographic features lead to a broad dispersion of resources forcing the owls to move long distances. In addition to the geographic distribution of habitats, low productivity of small mammals also may contribute to large owl ranges. Lindstedt et al. (1986) showed that home range size among carnivores is related to prey production. Results of our small mammal studies suggest that abundance of mice and voles is quite low compared to regions inhabited by boreal owls in Scandinavia. On our most productive snap-trap grid (an old spruce-fir forest), we caught an average of 8.3 voles/100 trap nights during a week of trapping each spring for 2 years. We also caught 5.6 shrews/100 trap nights, or 13.9 small mammals/100 trap nights. On the next most productive forest site, an old Douglas-fir forest, we caught 0.9 mammals/100 trap nights; this sample did not include any shrews. Our trapping rate at the spruce-fir site was less than snap-trap capture rates reported by Lofgren et al. (1986) and Korpimäki (1987a,c) during vole peaks during their studies of boreal owls in Europe. Lofgren et al. (1986) captured 16.6 voles/100 trap nights during vole peaks and 1.4 during low years when boreal owls failed to



breed. Similarly, Korpimaki (1987a,c) captured up to 18 voles/100 trap nights in Finland during peak vole years. During all years, our trapping rates in habitats other than spruce-fir were lower than those observed by Lofgren et al. (1986) during low prey years. The habitats with low abundance of small mammals dominate the landscape at Chamberlain. Spruce-fir forest covered about 6% of our study area, and old stands that may support the greatest abundance of small mammals constitute only a portion of the spruce-fir forest. These results imply that small mammals are not abundant across much of the study area.

Further evidence of low prey availability comes from our observations of boreal owl courtship feeding. Courtship for some boreal owls lasted for over 3 months. During much of this period the pair met at the nest site several times a week. We suspect that males provided courtship food during these encounters. Beginning up to 2 weeks prior to laying, the female occupied the nest cavity continuously, receiving prey from her mate. Apparently the female requires an extended period of inactivity to accumulate reserves for egg laying. Hirons (1985b) has shown that female weight prior to egg laying in the tawny owl is strongly related to nesting success. The small clutches laid by boreal owls at Chamberlain after such lengthy courtship reinforces our contention that boreal owls do not easily obtain sufficient prey from habitats at Chamberlain.

In addition to low abundance of prey in most habitats, the few productive, old spruce-fir stands are relatively small and dispersed. The broad dispersion of good foraging sites could force the owls to use large home ranges. Because of long travel distances between old spruce-fir patches, the owls may hunt extensive areas of poorer forest rather than moving directly from 1 spruce-fir stand to the next.

### Population Status

*Reproduction and Survival.*—Observations of low reproduction and survival

for boreal owls over 4 years in the RNRW contrast with estimates of demographic characteristics for populations in Europe. In the RNRW, completed clutches averaged 3.1 eggs (range 2–4,  $n = 11$ ), and fledging rate for nests that fledged young averaged 2.33 young (range 2–3,  $n = 6$ ). Nest failure was an important component of low production; 10 of 16 nests failed. In Europe, boreal owls produce far more young. In Finland, during a 13-year study, Korpimaki (1987a) observed an average clutch of 5.6 ( $n = 412$ ) and a fledging rate for successful nests of 3.9 ( $n = 445$ ). He observed clutches as large as 10 and fledging rates up to 8 young/nest. Nest failure averaged 23%. Solheim (1983b) reported an average fledging rate of 4.8 young from first nests of polygamous boreal owls in Europe and biandrous females produced up to 12 young in a year. In Germany, König (1969) reported fledging rates of 4 young/nest in good vole years and 2.3 in poor years. His results suggest that German boreal owls produce as many young in poor years as the average production we observed on our study area.

Adult survival in Europe also exceeds estimated adult survival in the RNRW, although estimates for both regions are based on limited data. Our most liberal assumptions lead to an annual survival estimate of 46%. Franz et al. (1984) as cited by Korpimaki (1988b) reported female adult survival as 78%, and Sonerud (1988:180) referred to his own unpublished data to estimate survival of 62%.

*Population Growth.*—Interpreting the consequences of the demographic characteristics in terms of population growth is difficult without combining reproduction, mortality, and age of first reproduction in a model to examine population trend. Therefore, we used simple Leslie matrix projection models (Leslie 1945) to examine population status during our 4-year study. These projections suggest potential patterns of population growth for the population studied but must be viewed as hypotheses rather than statements of actual trend.

To examine a range of potential sce-



narios, we examined 4 models based on our estimates of demographic parameters for owls at Chamberlain. Each model included 9 age classes (Korpimäki 1988b) with complete mortality at age 9. Using this model structure, age class 7 includes <1% of the population in all scenarios.

We first assumed all nests fledge 2.33 young/year, no nests failed, and all females breed each year raising 1 brood/year and fledge 50% female offspring. We also assumed all females breed in the spring following birth. Adult survival was set at 46% (see Reproduction and Survival) assuming all emigration observed during the study was complemented by equal immigration. Finally, juvenile survival was assumed equal to our estimated adult survival. This model led to a stable population ( $\lambda = 0.99$ ). The model assumed all nest failures observed during the study were human caused and, therefore, not representative of the population (we actually believe only 1 of 10 failures was human caused).

A more realistic model assuming some nest failure and higher juvenile mortality suggested negative population growth ( $\lambda = 0.65$ ). Juvenile survival was set at half the adult rate and nest failure at 23% as measured by Korpimäki (1988b) rather than the higher failure rate we actually observed. For this model all other population parameters were set as in the first example.

These 2 models suggested that lambda (finite rate of increase) approaches 1 only when demographic characteristics of the population are assumed to be more favorable to population growth than estimates from Chamberlain during our 4-year-study period. Fecundity was higher than we observed in this study. Fecundity rates estimated for the RNRW do not include radio-marked females that did not attempt to mate. Therefore, these are optimistic estimates.

Our estimates of survival have broad confidence intervals, and, therefore, we cannot place too much certainty on the mean value. We, therefore, ran 2 more models using the 95% confidence intervals

on the survival estimates used in the other simulations. Fecundity for all age classes was set at the average for all nests monitored at Chamberlain.

Using the upper limit on survival (91%) and assuming juvenile survival is half the adult rate results in slight positive growth ( $\lambda = 1.02$ ). When survival is set at 23% (the lower limit) and juvenile survival at half the adult rate, population growth is strongly negative ( $\lambda = 0.28$ ).

Although these analyses are based on limited demographic information from only 4 years, the pattern of population growth is supported by other information. Throughout their range, boreal owls prey almost exclusively on small mammals (Klaus et al. 1975, Korpimäki 1981, Schelper 1989), and breeding populations are limited by small mammal abundance (Lofgren et al. 1986, Korpimäki 1987a). During our investigations, small mammal populations were low relative to productive owl sites (Lofgren et al. 1986, Korpimäki 1987c). Furthermore, home range areas used by boreal owls were extremely large, implying limited prey availability (Lindstedt et al. 1986) and high energy expenditure.

*Local and Regional Viability.*—From these simulations, we suggest that if conditions during our study were representative of long-term patterns, and if our estimates of demographic parameters are accurate, the RNRW population may not be self-sustaining. We hypothesize that during good breeding years the population experiences modest positive growth, but, during poor years, population decline is significant. Under this hypothesis, the boreal owl population we studied, which occurs in a biological reserve (wilderness area), is a sink population, relying on immigration for continued existence (rescue effect, Brown and Kodric-Brown 1977).

On a broader scale, boreal owls may experience positive growth during most years in subpopulations that are more productive. Our current studies of boreal owls 80 km west of Chamberlain demonstrate higher mean clutch size over a 3-year period ( $3.6 \pm 0.34$ ) (G. D. and P. H. Hay-

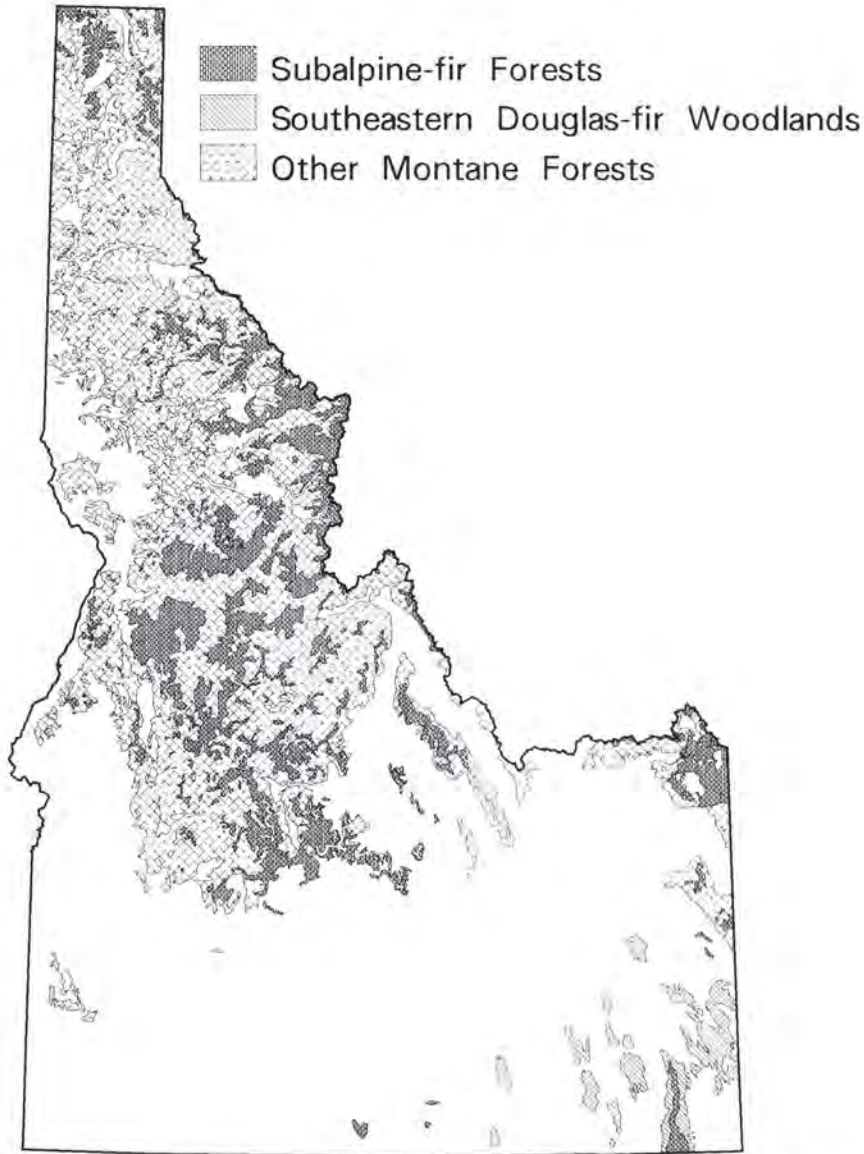


Fig. 6. Distribution of potential boreal owl habitat in Idaho based on results of regional owl surveys. Potential habitat is defined as forested sites in the subalpine-fir zone throughout the state and Douglas-fir woodland in southeastern Idaho. The map is based on data compiled by the Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, gap analysis program.

ward, unpubl. data). These more productive sites generally produce larger tree biomass and, therefore, are commercial forest lands where active forest management can be expected. Populations of boreal owls in wilderness, such as the RNRW, then, may in some situations depend on managed forest for long-term viability.

Therefore, the impact of silvicultural practices in productive spruce-fir forest may influence not only the local boreal owl population but also distant populations, including those in "biological reserves." Subpopulations of boreal owls throughout the northern Rockies may be linked in a loose metapopulation (Opdam 1991) through

juvenile dispersal and nomadic movements of adults.

Year-to-year movement patterns of boreal owls observed in the RNRW and in Europe would facilitate the dispersal required for the metapopulation dynamics we hypothesize. Wallin and Andersson (1981), Solheim (1983a), Lofgren *et al.* (1986), and Korpimäki (1986) have demonstrated that boreal owls in Europe exhibit both site tenacity and nomadic tendencies. In the most intensive investigation, Lofgren *et al.* (1986) showed that males were site tenacious throughout a prey cycle, whereas females were tenacious only during prey peaks. At Chamberlain, boreal owls showed a mixed strategy of site tenacity and nomadism (Hayward *et al.* 1987b). Clearly the owl's life history would facilitate recolonization of locally extinct habitats or the addition of individuals to sink populations through immigration. Production in some populations, however, must be sufficient to produce high net emigration rates.

### Regional Population Perspectives

Our sample of owl breeding sites throughout the northern Rockies suggests that boreal owls occur primarily in high-elevation (1,400–3,100 m) coniferous forest, especially spruce–fir. These forests cover only a small portion of the landscape and occur as isolates in the expanse of forested land (Fig. 6). Therefore, even in the absence of forest fragmentation from deforestation, subpopulations of boreal owls exist as geographic isolates potentially connected through movements of adult owls or dispersal of juveniles.

Information from U.S. Forest Service (USFS) timber database suggests the limited extent of potential boreal owl habitat in the northern Rockies. Although the accuracy of this database has not been validated, it provides a first approximation from which to draw general patterns. Within USFS Region 1, ~9% of the forest land supports spruce–fir forest 15-cm dbh or larger (J. W. Laux, Timber Manage-

Planner, Reg. 1, USFS, pers. commun.). On 7 forests in Idaho south of the Salmon River, spruce–fir forest covers ~7% of the forested landscape (H. A. Cheatham, Timber Manage., Reg. 4, USFS, pers. commun.). The spruce–fir forest within the region occurs in patches of varying extent separated from neighboring patches by landscapes supporting a range of vegetations (Fig. 6). The value of individual islands of spruce–fir forest to boreal owls will likely depend on the patch size, distance to nearest neighbor, vegetation (matrix) surrounding the patch, and the quality of habitat within the patch (MacArthur and Wilson 1963, Diamond 1975, Pimm *et al.* 1988).

How these landscape patterns interact to influence long-term viability of boreal owl populations is unknown. The limited extent of potential spruce–fir habitat suggests, however, that populations in this region may be vulnerable to reduction in suitable habitat (Stacey and Taper 1992). Loss of spruce–fir forest will reduce patch size, eliminate some habitat patches entirely, and increase the distance between suitable forest habitat. These processes have been linked to increased rates of local extinction (Connor and McCoy 1979, Burley 1989, Pimm and Gilpin 1989). Reductions in the size of forest habitat patches will likely reduce the numbers of owls in breeding populations. Because boreal owl populations inherently exist at low density (relative to passerines) and in this region may have low productivity and low survival, reduction in population size could lead to demographic instability and extinction due to stochastic events (Pimm and Gilpin 1989). Reductions in patch size also could lower the rate of immigration from neighboring populations, reduce the demographic linkage between populations, and potentially increase the rate of subpopulation turnover (Brown and Kodric-Brown 1977, Smith 1980). As pointed out by Stacey and Taper (1992), even suboptimal habitats may be important in maintaining persistence of a metapopulation. These habitats play a role in dis-



persal among subpopulations and as sites where floaters may exist prior to dispersal.

## CONCLUSIONS

Prior to this investigation, little was known of the biology of boreal owls in North America. Several results appear most important. Those include the following:

1. Boreal owls in the northern Rocky Mountains occur in a relatively narrow life zone, breeding predominantly in forests of the spruce-fir zone at elevations from 1,400 to 3,100 m. Regional geography and the species' limited elevation distribution together result in a natural distribution pattern with numerous breeding populations isolated on patches of high-elevation forest. Metapopulation dynamics, therefore, may largely influence local and regional dynamics and have important implications for management. Forest fragmentation and removal of mature forest habitats on a regional scale may harm boreal owl populations.
2. Although we could not directly study foraging habitat, evidence suggests that mature and older spruce-fir forest is important for foraging. The importance of these forests is especially significant considering the fluctuations in prey populations experienced in the life zone occupied by boreal owls. Based on our data, however, it is difficult to separate selection for roosting and foraging habitat.
3. In the RNRW, no single forest habitat provides optimum conditions for nesting, roosting, and foraging. The owls selected habitat that differed in structure from stratified random locations for nesting and paired random sites for roosting. Forests chosen for nesting and roosting provide different resources, each meeting special needs of the owls.
4. Local geography and habitat heterogeneity strongly influenced the daily and seasonal movements of boreal owls. Habitats with abundant cavities that provided optimum nesting habitat were

confined to low elevations on the eastern edge of the study area, whereas spruce-fir forest, which supported the highest prey populations and cool summer roosts, occurred at high elevations in the west. Therefore, resources used daily were not interspersed but segregated geographically.

5. Owls in the RNRW maintained large seasonal home ranges and moved long distances from day to day. The extensive movements result from several factors: the general low productivity of small mammals; dispersed distribution of habitats with abundant small mammals; and the distribution of habitats suitable for nesting, roosting, and foraging.
6. Boreal owl breeding populations and breeding success fluctuated during the study. These fluctuations may be tied to availability of small mammals, especially southern red-backed voles. The nature of fluctuations in demographic parameters has implications for assessing population viability and setting management guidelines.
7. Productivity of boreal owls in the RNRW is low compared to populations in Europe, and adult mortality may be high. Similar to populations in Europe, breeding populations and breeding success fluctuated during our study. Based on these demographic characteristics and results of Leslie projections, we suggest that this population is not self-sustaining. We hypothesize that the RNRW population may, in the long term, persist only because of linkage with a larger metapopulation.

## MANAGEMENT RECOMMENDATIONS

Results of our study should not be used to make inferences to boreal owls outside the populations sampled. We measured nesting habitat at sites in Idaho and Montana, but the majority of our results come from owls in the RNRW. Boreal owls in the RNRW appear to occupy unproduc-

tive habitat, and the patterns observed may or may not apply to populations throughout the northern Rocky Mountains. In an academic sense, then, until we investigate other populations in the region and examine boreal owl ecology in managed forest, we are uncertain how the owls will respond to changing environments in the region. The need for further research is obvious and we discuss priorities below.

The manager, however, must make decisions regarding forest management despite our limited understanding of boreal owl ecology. In the comments that follow, we have not attempted to develop a conservation plan but rather present basic management ideas based on the boreal owl populations we studied.

### Distribution and Abundance

Biologists should consider all forested sites in the spruce–fir zone (*Abies lasiocarpa*) as potential boreal owl habitat. Forests within 100–200 m elevation below this zone also will support breeding boreal owls and may be the most important nesting habitats. Playback surveys conducted from January to April offer the most efficient means of determining general geographic distribution patterns. A single year of negative results, however, does not constitute evidence that a site is not occupied. Absence can never be established, and the yearly variation in calling rates we observed suggest that several years of surveys will be necessary to establish presence or absence.

Any attempt to monitor trends in abundance or productivity will require development of specific monitoring methods. Playback survey methods developed for spotted owls (Forsman 1983, Thomas et al. 1990) should not be used to monitor boreal owl population trend. Spotted owls and boreal owls have different territorial systems (Mikkola 1983, Forsman et al. 1984) and, therefore, have different singing behavior. Because we do not understand what factors (aside from breeding density) influence singing rates in boreal owls, play-

back surveys are not a suitable intensive monitoring tool. The probability of an individual responding to playback depends on the time of night, current weather conditions, past weather conditions (that influence snowpack, plant phenology, and small mammal availability), the individual owl's physiological condition, degree of competition for nest sites from other male owls, and whether the owl has attracted a mate. Lundberg (1979) suggested that the number of boreal owls singing may be inversely related to breeding success. Despite problems in using playback surveys to monitor *abundance* of individual populations, playback surveys conducted each year, over a large region, may be useful in detecting regional trends by assessing population presence in numerous subpopulations. We are currently exploring the use of nest boxes to monitor owls on a local scale (Hayward et al. 1992). An acceptable monitoring scheme will require a valid sampling design conducted at a scale that matches the goals of the monitoring plan.

### Habitat Management

*Nesting Habitat.*—Management of nesting habitat will largely involve snag management, management of large woodpeckers, and aspen management. Maintenance of mature aspen stands dispersed across the landscape can be important in managing boreal owl nesting habitat. Even aspen stands that cover small areas are important because of the high use of aspen by primary cavity nesters including pileated woodpeckers (G. D. and P. H. Hayward, pers. obs.). Aspen should exceed 33-cm dbh, however, to support a cavity large enough for a boreal owl. In conifer forest, potential nest snags should be >38-cm dbh and part of a forest stand. Our evidence suggests that small stands, less than a hectare, are suitable. Snags in mature or older conifer forest or aspen stands should be retained. We recommend leaving clumps of trees around large snags within clearcut units in landscapes where timber harvest is extensive. Leave-strips along stream cor-

ridors should not be viewed as the major element of a network for potential boreal owl nesting habitat; few nest sites located in our studies were in low topographic positions. Because the owls do not defend large nesting territories, potential nest stands may be under 1 km apart.

In Europe nearly 90% of some populations nest in nest boxes (Lofgren et al. 1986). This proven tool may be necessary to maintain boreal owls on some forests. Before adopting boxes as standard management tools for degraded forest landscapes, however, we must evaluate how box dispersion, density, and other factors influence boreal owls and other members of the forest community. In Europe, predation at nest boxes is not uncommon (Sonerud 1985), and our experience with nest boxes indicates American marten predation at nest boxes can be high (G. D. and P. H. Hayward, pers. obs.). In any case, because nest-box programs ignore requirements of species other than the target species, nest boxes should not be considered a desirable mitigation tool for future timber-harvest operations but may be useful in mitigating past mistakes.

*Roosting and Foraging Habitat.*—Roosting habitat can be maintained through management of foraging habitat. Suitable winter roosting habitat appears to be met by any sawtimber or older coniferous forest. For summer roosts the owls need cool sites found most commonly in mature and older spruce–fir forests. Summer roosting habitat must be well dispersed because the owls use large home ranges and roost throughout their home range.

Managing foraging habitat will be the most important challenge to the forest manager. Boreal owls are food limited (Lofgren et al. 1986, Korpimäki 1987a), and reductions in prey availability would have negative consequences for populations in marginal habitat. Silvicultural prescriptions should be designed to maintain stands with abundant small mammals and stand structure that permits owl foraging flights. Clearcuts, large meadows, and young forest stands are not quality foraging habitat.

A variety of silvicultural treatments could maintain suitable foraging habitat. In each case, several objectives should be pursued: maintenance of some forest structure to facilitate hunting; prevention of dense thicket-like timber that inhibits owl mobility; and maintenance of a microenvironment suitable for small mammal populations, especially southern red-backed voles. Slash treatment should assure that large woody debris is maintained in the system for small mammals (Fogel and Trappe 1978, Maser et al. 1978, Martell 1981).

In cases where current stand structure and silvicultural objectives dictate an even-aged system, we suggest either an irregular shelterwood or group shelterwood system. In both systems, clumps of overstory trees are left after the preparatory and seed cuts. To promote owl foraging habitat, some of the clumps should be retained after the overstory removal. During the rotation, intermediate treatments that open the regenerating stand will facilitate development of suitable hunting conditions. In lodgepole-pine forest, where a shelterwood is not feasible, small-patch clearcutting is recommended using patch sizes that approach group selection techniques.

In older spruce–fir forest, uneven-aged forest management (such as group selection) would provide for owl foraging habitat and permit timber harvest. On spruce–fir land units allocated to timber production, some form of partial cutting is desirable from the perspective of many resources, including boreal owl habitat management. Although wood-fiber production in spruce–fir forest is low relative to other coniferous forests, watershed and aesthetic values are high. Partial cutting maintains these values and protects soil productivity (Alexander 1987). A wide variety of wildlife, including American marten (Buskirk et al. 1989), fisher (Jones 1991), and great gray owls (Bull et al. 1988b) also would benefit directly or indirectly from maintenance of forest cover.

“Although uneven-aged cutting methods—individual tree and group selection—have seldom been used in spruce–fir forests, they appear to simulate the nat-



ural dynamics of these forests" (Alexander 1987:59). Group selection systems are easier to design and therefore may be preferable, especially in stands that are naturally patchy. All tree sizes, including some very large trees, should be represented in the postharvest stand. This will assure production of large snags for nesting, large woody debris for small mammals, and clumps with high canopy cover for roosting.

A review of 14 national forest plans from Regions 1 and 4, however, demonstrates a reluctance to initiate uneven-aged management in many spruce-fir stands. Our interpretation of 14 plans in 1989 indicated even-aged management would dominate on all but 1 forest.

An acceptable alternative to group selection, which may be easier to administer and design, is small-patch or strip clear-cutting. To maintain forest structure suitable for owl foraging habitat, a portion of any harvested watershed (including areas outside the riparian area) should be managed on a long rotation. Mature stands should be well distributed through the watershed.

*Landscape Scale Perspective.*—Because boreal owls use large home ranges, population densities are low, and patches of suitable habitat are relatively small (Fig. 6), immigration is likely important to maintain individual populations (Stacey and Taper 1992). To facilitate movement between subpopulations, quality habitat must be well distributed throughout the species' geographic range. The area necessary to support a population is unknown but likely exceeds 1,000 km<sup>2</sup>. Throughout the landscape, only a modest (unknown) percent of the area must remain high quality foraging habitat, but quality stands must be well dispersed. In areas managed to support boreal owls, we recommend that a portion of a watershed be maintained in mature or older forest and over half be forested with stands older than saplings.

Many individual boreal owl populations must be maintained because of the small area occupied by each and, therefore, the potential probability for local extinction. Because spruce-fir forests are naturally

limited due to geography and fire history, the manager will be challenged to maintain suitable habitat to support the species in regions with high timber harvest.

## Research

An outline of research priorities must recognize that prior to our investigation only 2 ecological studies (Bondrup-Nielsen 1978, Palmer 1986) addressed boreal owl habitat use in North America. As a major avian predator of small mammals in spruce-fir forests of the northern Rocky Mountains, boreal owls play an important role in these forests. Study of small mammal habitat use and population dynamics should be a high priority. A wide range of predators (American marten, fisher, coyote, and forest owls) rely on relatively few small mammal species in spruce-fir forest. But, how *Clethrionomys* and *Phenacomys* populations can be managed through silvicultural treatments is unknown. The literature on habitat use by *Phenacomys*, in particular, is limited (McAllister and Hoffmann 1988).

Foraging habitat use by boreal owls must be investigated in managed forest to understand how the species uses stands of differing structure. We suggest an experimental approach that creates landscape level treatments on managed forest lands. Treatments should include even- and uneven-aged management systems comparing foraging behavior and productivity of owls using alternate treatments.

To assess the regional status of boreal owls, basic population demography must be studied. The goal should be a database sufficient to build demographic models of owl populations from several sites with varying productivity and survival. To build a reliable metapopulation model, information must be obtained on the extent of adult and juvenile movements. The ultimate goal must be a spatially-explicit regional metapopulation model. We are currently working on such an approach.

Finally, alternative methods to monitor populations and habitat must be explored. It may be impractical to monitor population trend for a species that naturally

exists at low densities in inaccessible habitat. Therefore, methods to efficiently monitor presence or absence and some measures of habitat quality may be most desirable.

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## APPENDIX

Vegetation characteristics recorded at boreal owl nest sites, potential breeding sites, and random sites in the Frank Church River of No Return Wilderness to evaluate habitat at breeding locations.

Variable	Measurement
% shrub cover 0-1 m high	Mean of 8 line-intercept transects
% shrub cover 1.1-2 m high	Mean of 8 line-intercept transects
% deciduous cover 2.1-4 m high	Mean of 8 line-intercept transects
% deciduous cover 4.1-8 m high	Mean of 8 line-intercept transects
% deciduous cover >8 m high	Mean of 8 line-intercept transects
% conifer cover 0-1 m high	Mean of 8 line-intercept transects
% conifer cover 1.1-2 m high	Mean of 8 line-intercept transects
% conifer cover 2.1-4 m high	Mean of 8 line-intercept transects
% conifer cover 4.1-8 m high	Mean of 8 line-intercept transects
% conifer cover >8 m high	Mean of 8 line-intercept transects
% cover grass	Mean of 16 0.1-m <sup>2</sup> -rectangular plots
% cover forb	Mean of 16 0.1-m <sup>2</sup> -rectangular plots
% cover subshrub	Mean of 16 0.1-m <sup>2</sup> -rectangular plots
Density trees 2.5-7.6-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees 7.7-15-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees 15.1-23-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees 23.1-38-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees 38.1-53-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees >53-cm dbh	Mean of 16 83-m <sup>2</sup> -circular plots
Density trees >30.5-cm dbh	Mean of 4 variable-radius plots
Basal area of trees >15-cm dbh	Mean of 4 variable-radius plots

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