HABITAT USE AND POPULATION BIOLOGY OF BOREAL OWLS IN THE NORTHERN ROCKY MOUNTAINS, USA

By

GREGORY D. HAYWARD

1989

HABITAT USE AND POPULATION BIOLOGY OF BOREAL OWLS
IN THE
NORTHERN ROCKY MOUNTAINS, USA

A Dissertation
Presented in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
with a
Major in Forestry, Wildlife, and Range Sciences
in the
College of Graduate Studies
University of Idaho

by
Gregory D. Hayward

August 1989

AUTHORIZATION TO SUBMIT
DISSERTATION

This dissertation of Gregory D. Hayward, submitted for the degree of Doctor of Philosophy with a major in Wildlife Resources and titled "Habitat Use and Population Biology of Boreal Owls in the Northern Rocky Mountains, USA," has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor E O Garton Date 8/8/89

Committee Members Ernest D. Ables Date 8/8/89

Leon F Neuenschwander Date 8/8/89

James M Peek Date 8 aug 89

Department Administrator Ernest D. Ables Date 8/8/89

College Dean Leon F Neuenschwander Date 8/10/89

College of Graduate Studies Final Approval and Acceptance:

____________________ Date ________

ABSTRACT

From 1984-1988 we studied habitat use by boreal owls in the Northern Rocky Mountains. Radio-telemetry studies of one owl population provided the bulk of our data. To explain the patterns of habitat use observed, we also studied owl population biology and habitat affinities of principal prey species. Boreal owls inhabited forests within the spruce-fir life zone throughout the mountains of Montana, Idaho, and northern Wyoming. Nearly 90% of potential nest sites in this region were in Abies lasiocarpa habitat types and no singing locations were found below 1292 m. At Chamberlain Basin, in central Idaho, owls nested in mixed conifer (40%), spruce-fir (18%), Douglas-fir (21%), and aspen stands (21%). Lodgepole pine forest, which was the most common forest type in the area, was not used for nesting. Nest sites were in old forest stands with complex physical structure. Roosting habitat differed between winter and summer. Winter roosts differed little from available forest cover while summer roosts had greater canopy cover, higher tree density, and higher basal area than paired random sites. The best foraging habitat was associated with older spruce-fir stands. These sites had higher prey populations than other sites as revealed by snap and pit trapping. Because of the wide dispersion of suitable nesting, roosting, and foraging habitat the owls used large home ranges; seasonal ranges averaged 1,451 ± 522 ha in winter and 1182 ± 334 ha in summer. Boreal owls at our intensive study site fed primarily on small mammals in both winter and summer. During both seasons red-backed voles where the most common prey.

Estimates of demographic characteristics of boreal owls at Chamberlain suggest that the population may not be self supporting but rely on emigration from other populations. We estimated annual adult mortality as 46% and production by nesting females averaged 2.3 young per successful nest.

These results suggest that conservation of boreal owls will require coordinated regional planning and changes in certain forest management practices. Regional planning must strive to maintain quality nesting, foraging, and roosting habitat in islands and connecting corridors well dispersed throughout the region. A shift to uneven age management of spruce-fir forest should meet the owl's needs for nesting structures, roosting sites, and maintain high prey populations.

ACKNOWLEDGEMENTS

I would like to express my most sincere thanks to my wife and colleague Pat Hayward for her dedication throughout every phase of this research. Pat secured funding, coordinated field work, wrote reports, and worked horrendous hours in winter and summer to gather the data responsible for any insights we've made into boreal owl biology. It may sound trite to those not involved but she at times risked serious physical injury in the interest of the project. In short Pat's name belongs on this dissertation beside my own. Only the traditions of society and economic realities prevent that.

Guidance from my friend, mentor, and advisor Dr. E. O. Garton meant more to the project and myself than he will ever admit. Oz's insight into study design and into population biology have been influential for the project and my development as an ecologist.

Support from our family during an isolated four years of field work gave Pat and I a treat to look forward to with every bi-monthly mail flight. Their eagerness to share our wilderness experience (through the mail connection) made our trivial day to day work seem more important. At least someone "out in society" cared if we learned something about the boreal owl.

I owe a debt to Lynn Flaccus, Tony Wright, and Dawn Zebley who worked tirelessly skiing and hiking the backcountry, collecting the data which made this study a success. Their understanding of the difficulties of wilderness research and willingness to put up with a student 'learning' to manage a field crew made working with them a joy. I also thank Russ Ryker who had the foresight and determination to take our initial proposal and convince the Forest Service that it was in their interest to learn how we can fit the boreal owl into forest management. I also thank the numerous biologists who cooperated in regional surveys for owls and Ron Escano for coordinating those surveys in Region I. The U. S. Forest Service Intermountain Forest and Range Experiment Station, Idaho Department of Fish and Game, University of Idaho Wilderness Research Station, Max McGraw Wildlife Foundation, North American Bluebird Society, TDK Electronics, Duracell Corporation, Richland, and Washington Audubon Society, provided funding; I thank each of them. Arnold Aviation provided safe air taxi service and companionship over the radio - thanks to Ray, Carol, Mary, all the pilots and crew. Finally I thank all of you who I have failed to acknowledge - please forgive me for my oversight.

DEDICATION

I dedicate this work to the wilderness and all wild places, those lands where man's mark is weakest and from which man can learn the most.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

This dissertation is written as a manuscript ready for submittal to a professional journal. As such, the format of the manuscript follows guidelines of *Wildlife Monographs*. The research was conducted with two other scientists, thus the manuscript will be submitted with multiple authorship and the personal pronoun "we" is used throughout.

INTRODUCTION

Understanding patterns of habitat use is central to the formulation of species conservation programs and to understanding species ecology. Land management agencies rely on models (verbal or quantitative) of habitat use to predict the consequences of management actions on wildlife species. Decisions concerning preserve design and the optimal location of preserves also rely on knowledge of species' habitat associations (Scott et al. 1987). Likewise, knowledge of habitat relationships aids in understanding factors which determine animal abundance, patterns of population change, causes of extinction, rates of colonization and other aspects of population ecology. Whether a species is tied tightly to specific habitat features or displays flexible habitat affinity influences much of its autecology.

A population's habitat relationships integrate diverse aspects of the species' behavior, morphology, life history, and the environmental setting. Breeding behavior, foraging behavior, physiologic tolerances, food habits, and population density all influence the range and type of habitat used by a population. Therefore, through the study of habitat use we can learn much about the population ecology of a species. Conversely, to thoroughly study habitat use we must also look at many seemingly unrelated aspects of a species' biology. For instance, to understand breeding habitat use we must understand the species' mating system; to understand foraging habitat we need information on food habits and foraging behavior. Of course, conclusions based on habitat use are limited to the environmental context of a particular study.

In this study we investigated habitat use by boreal owls (Aegolius funereus) in the northern Rocky Mountains of the United States. We approached the study of boreal owl habitat from a broad perspective by investigating the owl's natural history, as well as habitat use, 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 boreal 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. Similarly, boreal owl natural history, including breeding phenology, food habits, movement patterns, and population dynamics throughout this region, had not been studied.

Our goal was to describe habitat use by boreal owls at several scales and, where possible, to suggest reasons for the pattern observed. 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 and future status.

Our working model throughout the study was that boreal owls chose particular habitats from the range of available types such that survival and production were higher than if alternate habitats were used. We assume that the habitats most used by a sample of individuals represent the habitats most important to the species in this region or those habitats which lead to the highest average individual fitness. Random habitat use, we hypothesized, would lead to lower fitness. We sought to measure survival and reproduction by individuals to assess the value of the habitat (Van Horn 1983)

This general model, which simply states that habitat choice is directly related to fitness, underlies most habitat studies. Our study was not designed to test this model but the model served as a basis for study design and to interpret observations. Important assumptions include: 1) habitat is important in determining resources acquired, chance of being preyed upon, and environmental stress experienced, 2) the time spent in a habitat indicates the importance of that habitat for a given activity, 3) during periods of high population density intraspecific competition does not force individuals to use poor habitats, and 4) different individuals follow the same "model" of habitat choice.

Our working model, then, takes a traditional, equilibrium view of communities and resources. This traditional model follows ideas typified by MacArthur (1958), Fretwell and Lucas (1969), and Schoener (1982). Recently, Wiens (1985), Strong (1986), and others proposed an alternative non-equilibrium approach. Whether an ecologist adopts a traditional or modified view of communities can influence the questions asked during a study. We agree that patterns of habitat use have numerous causes (historic circumstances, environmental variation, species interactions, physiological limitations). We also expect that in some circumstances habitat use will be random. We do not believe, however, that adopting the traditional model as a starting point altered our conclusions. At that stage in the study of boreal owls, our primary goal was to describe habitat use, not to study the process of habitat selection.

STUDY AREA

Our extensive surveys for boreal owls and measurement of habitat at potential breeding sites covered portions of the Northern Rocky Mountains from northern Idaho and Montana to northern Wyoming and Utah. Cooperators surveyed for owls on 13 National Forests including the Idaho Panhandle, Kootenai, Flathead, Lolo, Lewis and Clark, Beaverhead, Nezperce, Payette, Salmon, Boise, Bridger Teton, Fishlake, and Caribou National Forests. These forests include a diversity of climate and coniferous forest in a broad geographic area. Owl surveys were restricted to coniferous forest but extended from lower to upper timberline on many forests.

We conducted intensive investigations on the first identified population of boreal owls in the northern Rocky Mountains. This population inhabited the mountains of central Idaho in the northern portion of the Frank Church, River of No Return Wilderness (RNRW). The intensive study area included about half of Chamberlain Basin, particularly the basin upstream from the junction of the West Fork and Chamberlain Creek, the area within about 5.5 km of Cold Meadows Guard Station, and the area within about 5 km of Hot Springs Meadow. Over 90% of our field work was in a 7000 ha. portion of Chamberlain Basin near the Chamberlain Guard Station.

Our wilderness study area lay between 1580 and 2402 m elevation in a high, dissected plateau surrounded on three sides by deep rocky canyons which plunge to 700 m elevation. The entire area is mountainous but lacks steep jagged peaks; few slopes exceed 50%. The Chamberlain Basin study site (here after Chamberlain) slopes eastward from a high ridge on the west. Streams cut through a series of north-south ridges as they flow east. Only the main Chamberlain Creek shows evidence of glaciation - otherwise valleys are V-shaped and open meadows or bogs are rare. The granitic soils are highly erodible and support low to moderate plant productivity (Steele et al. 1981).

Climate in the region has a strong Pacific coastal influence during winter but follows continental patterns in summer (Finklin 1988). November through February is the coldest period with the greatest precipitation in December and January. A second precipitation peak occurs in May and June. Clear skies dominate from July through September. At 1700 m elevation Chamberlain Basin Guard Station receives about 76 cm of precipitation a year - 50% as snowfall. Snow depths reach 50-90 cm at this elevation. At 2150 m 70% of precipitation is snowfall. The frost free period at the guard station lasts 35-40 days although in the valleys frost may occur any day of the year. In July, maximum temperatures average 79° F with average minimums of 35° F. Our records of daily temperature extremes recorded at the guard station in February over four years averaged 35° F maximum and 11° F minimum. The record low temperature during the study was -30° F at Chamberlain on 4 February 1985. These temperatures all correspond to the lowest elevation on the study area.

The landscape of the wilderness study areas is dominated by coniferous forests. Openings cover less than 3 per cent of the Chamberlain site. The patterns of forest structure and dominant overstory species results from a history of recurrent fires (Steele et al. 1981). Lodgepole pine (Pinus contorta) dominates the forest especially in cold air drainages where monocultures of this species cover extensive areas. Below 1825 m on southern aspects open forest of 60-130 cm Ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) occupy some slopes where fire has prevented Douglas-fir from forming a closed canopy forest. These old forests are called mixed conifer throughout this text. On cooler aspects up to 2000 m Douglas-fir dominates unless recent fire has produced a lodgepole pine forest. Some Douglas-fir extends up to 2200 m mixed with subalpine fir (Abies lasiocarpa) and Engelmann spruce (Picea engelmannii) but spruce-fir forest dominates above 2000 m on sites without recent fire. Some spruce-fir forest extends as low as 1800 m on the cooler slopes.

Aspen occur in small clumps (usually less than 0.5 ha) below 2100 m and cover less then 1% of the landscape at Chamberlain. Grand-fir (Abies grandis) forest does not occur at Chamberlain although individual grand-fir trees occur at densities which likely do not exceed 1 per km^2. Sage/bunchgrass slopes are the most common open habitat below 1850 m. The only extensive forest less than 50 years old at Chamberlain occurred at the far northwest edge of the study site; a 2225 ha burn which burned in 1966.

A surprising diversity of owls in addition to boreal owls inhabit the region. Northern Pygmy (Glaucidium gnoma), northern saw-whet (Aegolius acadicus), great-horned (Bubo virginianus), and great grey (Strix nebulosa) owls were heard each year. Barred owls (S. varia) were heard each year after 1984. Long-eared owls (Asio otus) were seen occasionally but may not nest in the area while Flammulated owls (Otus flammeolus) appear to nest most years in the mixed conifer stands at Chamberlain. Diurnal raptors may be less abundant than owls. Red-tailed hawks (Buteo jamaicensis), northern harriers (Circus cyaneus), and all three North American accipiters occur on the study area.

Two important primary excavators, Pileated woodpeckers (Dryocopus pileatus) and Common Flicker(Colaptes auratus), breed in the area but are most abundant in the lower elevations.

METHODS

PHILOSOPHY

We would like to begin by describing our approach to this study and the philosophy which guided our methodology. As mentioned earlier, when we began this study there were only 2 confirmed breeding populations of boreal owls in the Rocky Mountains south of Canada; one in northern Colorado (Palmer and Ryder 1984) and one in central Idaho (Hayward and Garton 1983). The distribution and ecology of the species in this region was unknown. We felt that information on regional distribution and habitat use were first priorities in development of a management strategy.

Habitat use could be studied at several scales, however, and no single study could pretend to pursue a deep understanding at all levels of resolution. Paradoxically, understanding habitat use at any single scale requires some knowledge of a species' distribution at coarser scales. We chose to explore habitat use at several levels: 1) regional -covering several states in the northern Rockies, 2) local - including 2 study areas, each encompassing over 6500 ha, 3) within home ranges - exploring choice of stands within the area of a home range, and 4) microsite - emphasizing characteristics in areas smaller than forest stands. We allocated our effort disproportionately by emphasizing habitat use on a fine scale through intensive study of a single population of boreal owls at Chamberlain Basin. Extensive studies of broad scale habitat use (life zones) on a regional basis defined rough distributional limits over a large geographic area. Through the extensive work we sought to define the range of forest types in which the species is most abundant.

Understanding a predator's habitat use requires knowledge of its life history, social structure, food habits, and density, in addition to the habitat use and availability of prey, and distribution and availability of any special habitat requirements. Although incomplete, this list underscores the enormous task of studying habitat use. We attempted to meet this challenge by intensively studying both predator and prey populations as well as boreal owl natural history and behavior at one study site, Chamberlain Basin, for 4.5 years. Of course, intensive study of more than one site could have allowed for broader extrapolation of results but the effort would have precluded study of prey populations and owl natural history. We felt this supporting information was necessary to interpret observed patterns of habitat use. We did strike a compromise by intensively studying nesting habitat at a second site, Cold Meadows located 55 km east of Chamberlain at 2133 m elevation.

Habitat use can be studied from a perspective of a vegetative continuum or classified communities. A majority of investigators classify habitats into a limited number of categories and search for evidence of selection using methods outlined in Alldredge and Ratti (1986). This approach dovetails nicely with classifications of habitat for management but is limited by sample size in the number of habitat categories which can be investigated. It also suffers from the inherent difficulties of placing continuously varying sites into strict categories. Other investigators measure habitat features as continuous characteristics and search for patterns in habitat use by employing discriminant analysis, multiple regression, principal components analysis or other analysis of continuous variables (Capen 1981). This second approach can be a powerful means of identifying particular habitat characteristics used by an animal but fits less easily into management schemes. Choice of habitat variables is critical in the second approach, and investigators often measure more variables than can be efficiently analyzed. Finally, both approaches are limited in that neither can predict habitat use in an area with a different mix of available habitats.

We chose to approach habitat from both perspectives - in some cases as a continuum and in others as distinct habitat categories - depending on the scale being studied. Broad scale habitat use was explored by classifying habitat into life zone or elevation categories, while specific microhabitat features were measured and analyzed as continuous variables. As the scale of interest became finer, our approach allowed closer examination of particular habitat characteristics.

DEFINITIONS

Several terms used loosely in the ecological literature are used throughout our text. We define them below.

Microhabitat refers to conditions within an area smaller than a forest stand - a site where an individual performs a single activity such as roosting, nesting, or foraging. Microhabitat defines a fine scale of habitat resolution, but even within microhabitat, habitat can be viewed at several scales (e.g. nest snag vs. forest surrounding a nest snag).

Macrohabitat here refers to characteristics of the environment in an area large enough to include an individual's seasonal home range. For boreal owls, the forest stands are convenient units of measurement for macrohabitat description as home ranges are composed of numerous forest stands. Macrohabitat then, generally includes several vegetation types and landforms and is quantified by the proportion of area covered by each.

Classification of forest age/structure is an especially confusing area of wildlife ecology. For instance, oldgrowth forest has not been adequately defined such that forests may be objectively classified. In fact, the term has been used so loosely that its meaning is currently quite obscure. We used the following working definitions of stand age: Young forest - forest with few or no seed producing individuals where seedling establishment is common and leaf area is increasing. Therefore, structurally a young forest stand is dominated by small trees which are growing vigorously. Immature forest - a forest stand in which establishment is significantly reduced and competition has resulted in tree mortality, but stand age structure is primarily a result of the major disturbance which created the stand. An immature forest, then, has an even age tree structure, recently produced snags, but few young recently regenerated trees. Mature forest - a stand which 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 treefall gaps created after stand establishment and an uneven age tree structure. Old Forest - a stand of forest vegetation whose age structure 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. Although these definitions could not be applied in a quantitative manner we used them to subjectively classify forest stands.

FIELD PERIOD

This document reports results of field work from 26 January - 28 September 1984, 26 January - 28 August 1985, 14 January - 12 October 1986, 16 February -23 August 1987 and from two weeks in both February and May 1988.

FIELD METHODS

Locating and Capturing Owls

We explored the distribution of boreal owls in the northern Rockies (here we refer to the Rocky Mountains south of Canada and north of $42^{O}N$) using winter surveys in Idaho, Montana and isolated areas in Wyoming and Utah. Between February and April in 1984-1986 over 60 cooperators, primarily U. S. Forest Service biologists, searched for boreal owls by foot, car, and snowmobile using playback of tape recorded calls. Personnel from 13 National Forests, Grand Teton National Park, Wyoming Game and Fish, and the Garnett District of the Bureau of Land Management completed over 130 surveys covering nearly 1300 km through forest habitats from 500 to 3,050 m elevation, the majority being above 1280 m. Forest cover in survey areas ranged from Ponderosa pine at the lower elevations to lodgepole pine and spruce-fir at the highest sites.

In the RNRW, we used similar playback surveys to determine the elevation distribution of boreal owls and to locate individual breeding sites. All wilderness surveys were conducted on skis at night from January through April. Beginning just as the first stars became visible we played tape recordings of the boreal owl staccato song at 0.5 to 1 km intervals along trails and ridge lines. We remained at each calling station 10-12 min playing 3 series of staccato song with 2 min of silence after each series. In addition to time spent listening for owls at each calling station, we paused for one minute at least once between stations. Survey routes sampled available habitat radiating for about 10 km from our field lodging. The distance covered increased from the first through the third year. 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 one of 3 criteria: 1) we located an active nest, 2) we heard both a male and female boreal owl courting at the site, or 3) a male was found singing at the site on more than one night.

Habitat

Breeding Habitat--We described the structure of forest stands at confirmed nest sites and potential breeding sites (male calling locations) by measuring forest vegetation, topographic features, and habitat type on a macroplot within the nest or singing stand. The macroplot, which measured about 26 by 125 m, was located 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 macroplot 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 which did not actually exist. Within the macroplot, forest structure was quantified by percent cover of trees, shrubs, and herbs, and density of trees as described below.

Cover of trees and shrubs was sampled along 8, 30.5 m (100 ft) parallel transects placed perpendicular to the slope within the macroplot. Transects were randomly spaced 6-30 m apart. Intercept measurements along these transects provided tree and shrub cover estimates in 5 height categories (0-1 m, 1-2 m, 2-4 m, 4-8 m, >8 m). We recorded the dominant tree species and number of trees and snags in 6 dbh classes (2.5-7.6 cm, 7.6-15.2 cm, 15.2-22.9 cm, 22.9-38.1 cm, 38.1-53.3 cm, and >53.3 cm) within 16 systematically located 83 m^2 (0.02 ac) circular plots, 2 per transect. Cover of forbs, grasses, and subshrubs (any woody plant species commonly under 15 cm tall) was estimated on 16, 0.1 m^2 rectangular plots (Daubenmire 1959), 2 plots per transact.

Because the small (83 m^2) sample plots would underestimate numbers of large diam trees, variable radius plot tree samples were gathered from 4 points in the macroplot. We used a relescope with a 10 factor prism and 30 cm (12 in) dbh lower limit to count trees. Densities and basal area were calculated as described by Avery (1975:170).

We characterized forest vegetation structure on each site by computing averages for canopy cover by height category, tree density by dbh class, and herbaceous cover in 3 categories forb, grass, and sub-shrub. Mean tree density was calculated using only those plots which had trees. Topographic characteristics were described by major and minor aspect, slope, topographic position and distance to water.

We measured breeding habitat, as described above, at owl locations in the RNRW and boreal owl 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 Habitat Structure.--To describe the range of forest vegetation structure available at the Chamberlain study area, we measured characteristics of 101 random sites. Our objective was not to sample habitat in proportion to its availability but rather to adequately describe the full range of forest physiognomy of all cover types occupying 5% or more of the study area. Four cover types (lodgepole pine, spruce-fir, mixed conifer, and Douglas-fir) together represent over 99% of the forest cover in the study area. We chose 25 random points in each type from throughout the study area (26 in mixed conifer by mistake) using a random number table and UTM grid.

Sites were placed in one of the 4 types by overstory species composition. At each site we measured structural features of the vegetation which could influence owl mobility or which might be used as proximate cues by the owl when searching forest suitable for nest cavities or prey. Therefore, we measured forest structure to define the physiognomy of each stand. Methods followed those described above for breeding habitat except we used only 4 transects and all variables were measured with half as many subsamples.

Nest Tree and Microsite.--At each confirmed nest site, we recorded characteristics of the nest cavity, nest tree, and forest stand immediately around the nest. Nest cavity measurements included entrance diam (vertical and horizontal), cavity depth (vertical from base of cavity to bottom of entrance hole), cavity width, tree diam at cavity, cavity aspect and cavity height above the ground. Cover around the cavity was defined by measuring distances to the nearest foliage above, below, and to the sides of the cavity and assigning a cover rating from 1 (no cover) to 5 (dense cover) in each of these directions.

Forest structure within 2 concentric plots (5.2 and 11.4 m radius) around the nest was described by measuring tree density, canopy cover, and basal area as described under Roost Habitat. We also recorded dominant tree species, canopy height, distance to nearest opening, and distance to ecotone.

Cavity Availability and Nesting Habitat Structure.--We explored the roles of vegetation structure and cavity availability in nest site selection by boreal owls with a nest box experiment. Fifty wooden nest boxes hung within a 9 km^2 portion of the study area provided suitable nest structures in all forest types other than riparian forest stands. Nest boxes measured 44 cm high, 25 cm wide, 18 cm deep, and had an entrance 9 cm diam.

Three broad forest categories dominated the experimental area, old mixed conifer forest (dominated by ponderosa pine), mature and older Douglas-fir, and lodgepole pine. Reconnaissance revealed that these types varied in the availability of natural cavities suitable for boreal owls. Our surveys throughout the experimental area in 1980, 1981, and 1984 also indicated significant differences in boreal owl nesting across the 3 forest types. Lodgepole pine forest lacked suitable natural nest cavities although tree diameters exceeded the minimum necessary for boreal owls, and we observed no nesting or calling in this type. Due to the rotting characteristics of Douglas-fir, few suitable natural cavities were observed in this type, and we documented no nesting or calling by boreal owls in Douglas-fir. In contrast, natural cavities were abundant in mixed conifer forest and a majority of the observed boreal owl nest sites and calling locations occurred in this type.

The distribution of nest boxes formed a rough grid with a minimum of 500 m between grid points and 2 boxes near each point. The paired boxes were placed roughly 100 m apart and hung 3-15 m high. Boxes were placed on north or east sides of the tree bole unless overstory canopy would otherwise shade the box from afternoon sunshine. We checked and cleaned boxes of debris each spring during June.

We sought to design a small mensurative experiment in which vegetation type represented a treatment and each nest box was an independent observation repeated over 5 yrs. This design was not possible because of the distribution of vegetation and logistical constraints of working in wilderness. Interspersion of treatments, an important component of a well designed experiment (Hurlbert 1984), was not possible due to the distribution of forest types in the study. Therefore, the treatment of interest (forest type) was confounded with geographic location in our design. Also, because nest boxes were spaced closer than any inter-nest distances observed during the study, nest boxes were not completely independent. Thus, in years when a box was used, neighboring boxes were not considered available.

Roosting Habitat.--We located owls on their daytime roosts through radio tracking during all seasons. We tried to locate each owl twice a week on its daytime roost during our field seasons. Fewer roosts were found in autumn than other seasons. For purposes of quantifying roost habitat, if an owl moved after being located, the first roost perch observed was defined as the roost. Measurements taken at each roost sought to quantify the degree of cover provided by the roost tree and surrounding vegetation, to record site characteristics which would influence microclimate, and to classify the forest stand by habitat type (Steele et al. 1981).

While observing the roosting owl we recorded: aspect, slope (using a clinometer), topographic position, snow depth, dominant tree species (i.e. the most abundant species), and height to canopy. For the roost tree we recorded: distance to nearest opening and its size, tree species, dbh, height of lowest foliage, tree crown diam, tree height, perch height, and structure (open, closed, dense, or witch's broom). On a scale of 1 (no cover) to 5 (dense cover), we estimated cover above, below, and to the sides of the owl. In addition, we recorded aspect of perch from bole, aspect the bird was facing, direction of wind, wind speed at roost and in the open, temperature at the roost and in the closest opening (both recorded 4.5 ft above ground level in shade), distance from the owl to the bole, distance to nearest foliated branch above, below and to the side of the owl, as well as percent of cloud cover, and percent of snow cover in the open and percent of snow cover under the canopy. We wrote a short, narrative description of the vegetation in the immediate vicinity of the roost. After searching for a pellet, we flagged the tree.

Later, in the summer (from 1 day to 18 mo later), we returned to approximately 67% of the roost trees. We systematically eliminated every third roost for structural measurements. After a thorough search for pellets under the roost tree and under nearby adjacent trees, we collected tree density data from 2 concentric circles centered on the roost tree. Plots measured 5.2 m and 11.4 m radius and trees were counted in 7 diam classes: 2.5-7.6 cm, 7.6-15 cm, 15-23 cm, 23-38 cm, 38-53 cm, 53-68 cm, and >68 cm dbh. We also counted the number of snags in the same diam classes on the combined plots and estimated the height of the tallest tree in each plot. We measured overstory canopy cover using a modified forest densiometer. Holding the densiometer at waist height, the number of 17 points obscured by foliage were 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 greater than 15 cm dbh using a relescope and 20 factor angle centered at the roost tree. The roost tree was excluded from basal area calculations. We also recorded habitat type (Steele, et al. 1981).

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 random tree, we first turned a compass dial to determine the number of paces to travel (constrained to 30-180). A second compass spin indicated direction to walk. After pacing off the distance in the desired direction, the closest tree became the new plot center.

Small Mammal Habitat Use and Relative Abundance

To determine the relative abundance and species composition of small mammals and to discern any trend in small mammal densities between years, we inventoried small mammals at Chamberlain from 1984-1988. Inventories consisted of snap trapping grids run each spring and pit-trap sets established during spring 1985 and monitored through August 1988. Constraints on time, personnel and equipment precluded a thorough assessment of small mammal density and distribution. 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 x 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, one grid was placed in each of 4 vegetation types; bunchgrass/sagebrush, Carex wet meadow, lodgepole pine forest, and old mixed conifer forest. We placed trapping grids in stands of relatively homogeneous vegetation at least 30 m from an ecotone. In 1985, the same sites were trapped in the same order with one exception. The Carex wet meadow, a pasture used by U. S. Forest Service stock, was replaced with a less disturbed meadow which 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 were repeated 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 at the ends and center of a 3 m long, 15 cm high, sheet metal, drift fence (Williams and Braun 1983). 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, sage-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 (3 in wet old forest bottoms and 2 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 to 70 m from the snap trap grid within the same vegetation type.

STATISTICAL ANALYSIS

In this investigation we studied boreal owls using an approach which might be labeled quantitative natural history. Except for our manipulation of cavity availability within a small area at Chamberlain, our methods were completely observational, rather than experimental. Therefore, the knowledge obtained through our approach can be used principally to describe patterns, not to explain processes (James and McCulloch 1985). We will use our data to describe patterns of habitat use, food habits, and habitat use by owl prey populations.

We should place some limits on our study by defining the population of boreal owls studied and describing the level of confidence we feel the reader should place on our results. In different portions of our study we sampled owls from different populations. The majority of our observations come from a single population of owls in Chamberlain Basin. Nesting habitat used by boreal owls, however, was sampled at Cold Meadows and from sites on five National Forests in Idaho and Montana. We can, therefore, define a minimum range of habitats and forest types used for nesting by owls in a large region but other results can only be applied to the population at Chamberlain. Until the biology of boreal owls is observed in other locations we do not feel the patterns we observed can be ascribed to populations other than those actually sampled.

Throughout our results we frequently use statistics simply to describe patterns by presenting means or medians and a measure of dispersion. In these cases we feel simple description gives the most honest representation of our observations. Due to limitations in sampling, tests of statistical hypothesis would be premature for portions of our data. In other parts of our analysis we have applied the principles of experimental design to observational data to test for differences (James and McCulloch 1985). In these cases we feel the sampling procedures were adequate to apply statistical tests and draw weak inferences. Strict application of sampling theory was not possible in any aspect of this study and therefore any $\underline{P}$ values we calculated should be considered approximate. We do feel, however, that reasonable confidence can be placed in our results as they apply to the populations we sampled.

In this section on statistical methods we describe only the more elaborate analysis. We include descriptions of simpler statistical methods with the results so the reader can follow the way we built our analysis from one set of results to the next. All bounds reported are 95% bounds unless otherwise specified and $\underline{P} < 0.05$ was considered significant.

Boreal Owl Habitat Analysis

Nesting Habitat RNRW.--We compared the structure of forest vegetation in 101 random forest stands with 33 boreal owl nesting or calling sites using Principal Component Analysis (PCA). 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 therefore decided to run PCA without transforming any variables for two reasons. First, with over 100 samples for our ordination we felt comfortable invoking the Central Limit Theorem. Second, Johnson and Wichern (1982:362) indicate that ordination by PCA does not require a multivariate normal assumption. Because we measured different characteristics of forest structure in different units (cover in %, density in no./ha), we transformed all variables to Z-scores prior to analysis

(Pielou 1984). We entered 21 variables into PCA using 101 random forest sites. We used the eigenvectors from this analysis to calculate principal component scores for boreal owl use sites. We then plotted the random and use sites along the gradients defined by PCA.

We chose PCA rather than other ordination techniques because PCA works best when used on a relatively narrow range of habitats without any discontinuities. Otherwise, nonlinearity in the habitat variables will lead to distortion in the gradients defined by PCA (Orloci 1979). In cases where one has measured a broad gradient, detrended correspondence analysis may be preferred (Gauch 1982). Some (Wartenberg et al. 1987) feel the rescaling of axes in detrended correspondence analysis is rather arbitrary and if problems with nonlinearity are not expected, PCA is a more objective technique. Because our ordination included only forest habitats within a small geographic area in a narrow elevation zone, we felt the gradient being analyzed was rather narrow and PCA would perform well.

Roost Habitat.--To test whether boreal owls choose roost sites with different microhabitat structure than forests in the vicinity of roosts we used a multivariate paired-T test (Hotelling's T^2, 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.

In examining the influence of weather variables on the choice of the roost perch, we were most interested in whether the season, wind speed, wind direction, and air temperature influenced the aspect of the perch. The degree to which these factors influenced choice of perch would suggest to what extent behaviors related to thermoregulation govern perch selection and, therefore, in a general way, the degree of thermoregulatory stress placed on the owl.

Compass bearings are difficult to deal with statistically because of the circular scale of measurement. We dealt with the problem in 2 ways. Compass bearings were transformed to categorical variables and analyzed using chi square analysis as is often done. This analysis suffers from several problems. It is difficult to test for interactions among several variables simultaneously without enormous sample sizes. Sample size also limits the number of categories defined for each variable further limiting how closely interactions can be examined. We, therefore, looked only at 2-way contingency tables with several levels of each variable rather than 3-dimensional or larger tables.

Our second approach to the problem of a circular scale of measurement was to perform tests using the absolute difference between owl perch aspect and wind aspect as our dependent variable. For example, if an owl perched 350^0 with respect to the bole and the wind was blowing toward 15^0, the difference, 25^0, would be used in statistical tests. For chi square analysis, we grouped the difference into 4 categories: 1) 0-20°, which represents all cases in which a boreal owl perched next to a 25 cm dbh tree would be shielded from the wind, 2) 20-46°, which represents cases where up to half of the owl would be exposed to wind, 3) 46-90°, which represents cases where the owl is completely exposed to wind from the side, and 4) 90-180°, which represents roosts on the windward side of the tree.

Home Range and Owl Movements

In the analysis of distances between roost sites used on consecutive days, the sampling units were mean distances for individual owls. The measurements of distances between roosts were considered subsamples and mean distance between consecutive roosts was calculated from these values.

Home range size and boundaries were calculated using the program HOME RANGE (Samuel et al. 1985) which computes home range estimates using three methods; a modification of Dixon and Chapman's (1980) harmonic mean, Jennrich and Turner's (1969) bivariate normal ellipse, and the minimum convex polygon. Because the latter 2 estimates are not distribution free, we tested the distribution of owl relocations against the assumed distributions. Because over half the owl home ranges differed from the assumed distribution for either the bivariate normal or minimum convex polygon, we rejected those methods. We would prefer to estimate utilization distributions using a kernel estimator (Garton, in prep.), however programs for this method were not ready for general use at the time of analysis.

Prior to home range analysis we screened the input data for outliers, observations representing distant excursions from an owl's normal activity areas. Extreme observations inevitably plague home range studies (Schoener 1981). Outliers in a bivariate test, 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 less than three days, the point was removed.

Throughout our analysis we divided our field season 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 (we began field work in January) until over 50 percent bare ground was exposed on level ground at 1800 m, (about 1 May).

RESULTS

As stated earlier, our results include diverse aspects of boreal owl biology. The results begin with observations of boreal owl biology and then describes prey populations. The sections on biology begin by describing distribution and nesting habitat, roosting habitat and behavior, and owl movements and home range use. We then describe food habits and finally population characteristics including trends in abundance, mortality rates, and reproduction rates. The sections on prey populations include descriptions of trends in abundance and vegetation associations of small mammals.

HABITAT USE

Regional Habitat Use

Our discussion of regional habitat use refers only to nesting habitat because our sampling method, playback surveys, can only locate potential breeding areas. The results, however, indicate which life zone the species occupies and defines regional breeding distribution.

Forty-nine boreal owl nests and singing male owls were found in subalpine-fir, Engelmann spruce, western hemlock (Tsuga heterophyla), and Douglas-fir habitat types at sites throughout the northern Rocky Mountains

(Hayward et al. 1987a). All owl locations were found within the subalpine-fir life zone or within 100 m elevation of the subalpine-fir zone in mixed conifer or aspen stands. Forest cover types at owl locations 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%). Topographic position of owl locations varied considerably, ranging from bottoms to upper slopes. Biologists located owls singing in forest stands with aspects in each cardinal direction. Boreal owls were not heard below 1292 m (4240ft) elevation and 75% of the locations were above 1584m (5200ft). The sites below 1645m (5400ft) were all north of 48°N latitude.

Biologists classified 76% of the forest stands where they heard boreal owls as mature or older. The exceptions were lodgepole pine stands on the Beaverhead National Forest in drainages where lodgepole was the only coniferous forest type. These lodgepole sites appeared to support the largest trees in the area. On one lodgepole site, 404 trees per ha (163/ac) exceeded 23 cm dbh and 15 per ha exceeded 53 cm dbh. Each of the lodgepole sites we visited on the Beaverhead National Forest was marked for sale suggesting they represented the largest trees in the drainage. Boreal owls were never heard singing in even-aged, young forest stands in a survey region where mature forest stands were available. Over 50% of the boreal owl locations we visited outside the Wilderness were marked for timber sale.

Regional Microhabitat Use

Available habitats throughout the extensive region surveyed for boreal owls varied enormously. Overstory cover ranged from dry Ponderosa pine near Salmon, Idaho to spruce-fir bogs in northern Montana. Owls sang from stands with a wide variety of structure. On the Beaverhead National Forest where multi-storied forest with a complex structure was not available, owls sang in even-age lodgepole pine monoculture. These lodgepole stands were open and included some large trees (>38 cm dbh). Density of trees over 23 cm dbh on 3 sites averaged 260 per ha (104/ac) with 778 (314/ac) smaller trees per hectare. The presence of calling owls on these sites demonstrated that boreal owls will use forest with a simple structure. Aside from these lodgepole pine sites, boreal owls were only heard calling from stands with some components of mature forest; several canopy layers, numerous large trees, or several age classes of trees.

To summarize the range of forest structures used by owls in the Northern Rockies, we divided the 22 sites where we measured stand structure into 2 groups. 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. As expected, stands used by boreal owls in the northern forests had higher basal area and more large trees. In both regions, however, owls used some stands with low basal area and few large trees. Extreme and average characteristics of forests used in each region are displayed in Table 1.

Nesting Habitat Use in the RNRW

Available Forest Structure.--Prior to sampling stand structure we subjectively classified vegetation within the study area into 4 cover types based on dominant overstory tree species. Measurement of structural features at 25 sites in each cover type indicated that each overstory type exhibits some distinct structural characteristics while other structural features are not correlated with the overstory species. The species of dominant overstory, then, determines some aspects of forest structure but not others.

Lodgepole pine, mixed conifer and spruce-fir forests (but not Douglas-fir) could be distinguished from one another by a combination of understory canopy cover (conifer cover 0-4 m above ground) and basal area of large trees (>30 cm dbh). Lodgepole pine stands had low basal area and little understory canopy. Spruce-fir forest exhibited a broad range of basal area but differed from lodgepole and mixed conifer stands in greater understory canopy (Table 2). Mixed conifer stands had less understory canopy than spruce-fir but greater basal area. The range of Douglas-fir stands overlapped broadly with the other types, especially mixed conifer.

The 4 vegetation types differed in some structural characteristics while there was little correspondence between vegetation type and certain other structural features (Table 2) especially overstory cover. Thus, sites cannot be adequately described simply through classification by overstory.

Principal components analysis (PCA) of 101 random stands produced a more tractable description of the structural gradients available in the study area. With 21 structure variables PCA defined 6 principal components 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. Each of the 6 had an Eigenvalue larger than one (Table 3).

The 6 principal components retained for further analysis each described an ecologically interpretable gradient. The first component, described a complex gradient from highly structured, mature and older forest with many canopy layers to sapling pole timber with little vertical diversity. This component describes the overall physiognomy of the stand whereas subsequent components appear to relate to individual features of forest structures (i.e. understory, overstory). The second component is a gradient with relatively heavy cover 0-2 m above the ground, numerous 2.5-15 cm dbh trees and few large trees describing the positive end. A cline of large trees (>53 cm dbh), high basal area and upper canopy cover is defined by the third component. The fourth component defines a gradient in sawtimber size trees (15-38 cm dbh) with a strong upper canopy. The positive end of the fifth gradient includes stands with large snags (>38 cm dbh) and little grass cover. The final component is a simple gradient in forb ground cover.

A combination of principal components 1 and 2 effectively separates spruce-fir, lodgepole pine and mixed conifer stands (Fig. 1). The simple structure of lodgepole pine stands compared to other types is evident in Factor 1 where as spruce-fir and mixed conifer differ most in understory cover, Factor 2. Douglas-fir forest ranges 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 Factors 2 and 3. Like other forest types, lodgepole pine exhibits a range of understory conditions and a range of overstory densities. Unlike some regions of the Rockies, multiple-canopy-layered lodgepole pine forest is common in the study area. Components 4, 5, and 6 further demonstrate that classification by forest overstory type conceals much of the variation in forest structure; the 4 types are intermixed on many of the structural gradients defined by PCA.

Relationship of Owl Use to Available Forest Structure.--Did boreal owls in the RNRW show evidence of nonrandom choice in 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 singing locations and nest sites were found in mixed conifer (39.4%), spruce-fir (18.2%), Douglas fir (21.2%), and aspen (21.2%) stands. Lodgepole pine 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 types in proportion to their availability. Because of the geographic distribution of vegetation types, spruce-fir was under sampled during owl surveys the first 3 years of the study and lodgepole pine likely over surveyed. Despite these problems, the high use of aspen, which accounted for less than 1% of forest vegetation cover, suggests strong selection for some components of aspen stands. The lack of nests in lodgepole pine demonstrates avoidance of the most abundant forest type in the basin.

We plotted boreal owl singing locations and nest sites with random sites on the first 6 principal components described above to explore the pattern of use in relation to the range of available types. Boreal owls used complex, highly structured forest stands (Component 1) with less understory development than many available sites (Component 2, Fig. 2).

The distribution of used sites on Component 2 is especially striking. Owls used a broad range of sites on the lower end of the gradient with virtually no use above the average for available sites. Owls nested in stands with a broad range of overstory cover and large tree densities (Component 3) closely matching the full range of available types. Likewise, owl use sites showed no consistent selection for sites along the gradient of sawtimber tree densities (Component 4), or the gradient defined by component 5. Owl use concentrated on sites with above average grass-forb cover (component 6) although the majority of use sites were near the center of the range of available stands (Fig. 2).

We feel most comfortable applying PCA as a descriptive technique. Visual inspection of the pattern of habitat use on structural gradients suggests those habitat features where the distribution of use differs from the available range. Lack of conformity in used and available habitat can be recognized in both location and dispersion parameters of the distribution of habitat features on each structural gradient. Thus, the technique is a powerful descriptive tool and insights can be gained without inferential statistics. For those biologists who feel uncomfortable without a $\underline{P}$ value, we present the following tests. We tested for differences in random and use sites on each of the 6 components using T-tests. The mean principal component score for used and random sites were significantly different for components 1,2 and 6 ($\underline{P}$=0.0002, $\underline{P}$=0.0001, P=0.0085, respectively). There was no difference for components three ($\underline{P}$=0.580), four ($\underline{P}$=0.352) or five ($\underline{P}$=0.691).

<u>Description of Owl Use Sites, RNRW</u>.--The above analysis suggests that boreal owls choose nest sites in a non-random manner; the physiognomy of owl use sites did not encompass the full range of available types. Nesting and calling sites never occupied dense even-age forest or young forest stands. As discussed further below, boreal owls never nested in lodgepole pine forest - the most abundant cover type in the study area. The most characteristic structural features of 33 nesting and calling sites were a relatively high density of large trees (> 38 cm dbh), open understory, and a multi-layered canopy (Table 4).

The principal components analysis described above showed that compared to available sites, used stands had a complex structure with high basal area, trees in a variety of size classes, a developed forest canopy at several height zones, and high horizontal diversity (component 1). Use stands also had fewer small size trees and less canopy cover in lower height zones than random sites (component 2). Although the owls nested and called on only a subset of the available cover types, the range of forest types used was still quite broad. Of 28 use sites (several stands were used in more than one year by different owls), 11 occupied old, mixed conifer stands, 5 occupied aspen groves, 5 occupied old Douglas-fir forest, and 7 were in or near old spruce-fir forest.

All but 2 of 23 nest sites had extensive forest around the nest tree. One nest in 1987 occupied the dead top of 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 17 cm dbh spruce. This nest failed 15 days after hatching of 3 young. The second unusual nest occupied a Douglas fir snag in a 0.5 ha island of mature trees 20 m from extensive spruce fir forest.

We measured stand size for the other nest trees defining the stand as the area of forest with homogeneous overstory species and size class. The size of nest stands ranged from 0.8-14.6 ha and averaged 7.6 ± 3.96 ha. All 5 aspen nest stands ranged between 0.8 and 1.3 ha while the smallest coniferous forest nest stand covered 1.6 ha. All of these stands were surrounded by extensive forest.

During 4 years in the RNRW we heard many boreal owls that we were unable to locate precisely enough to measure microhabitat features. These less precise locations do, however, provide further evidence with which to describe boreal owl nesting habitat. At Chamberlain Basin we heard boreal owls calling at 24 additional sites. Only 2 of these were thought to be calling from a lodgepole pine stand. In neither instance was the bird close enough for us to be certain of its location. In both cases repeated surveys did not relocate a boreal singing in the area. Forest cover at 22 other (questionable) locations included 2 spruce-fir, 5 Douglas-fir, 6 aspen, and 9 mixed conifer stands.

We surveyed for boreal owls at Cold Meadows, in the RNRW, in 1984 - 1986. Each year we surveyed for 2-5 weeks. Cold Meadows, at 2121 m elevation, located 25 miles east of Chamberlain Basin, is dominated by lodgepole pine (60% lodgepole) and has more extensive wet meadows. We heard boreal owls call in 3 mature or older spruce-fir stands, 3 mature or older Douglas fir stands, and 2 mature or older mixed conifer stands. Boreal owls were not heard calling in lodgepole pine stands despite numerous common flicker nest cavities in large lodgepole pines along the meadows.

Working from cabins at Chamberlain and Cold Meadows did not provide convenient access to extensive spruce-fir forest. Cabins at Chamberlain were 6 miles from extensive spruce-fir forest which grow above 1830m in the basin. The rich fire history of Cold Meadows had left only small patches of spruce-fir forest. By 1987, however, our radio-telemetry results indicated the importance of spruce-fir as foraging and roosting habitats (reported below). We, therefore, sought to survey spruce-fir forest near Chamberlain Basin for evidence of nesting. In 1987, we heard 3 owls in mature or older spruce-fir forest near Hot Springs Meadow during 30.4 km of surveys on 5 nights. Surveys on 6 nights above Trout Creek, west of Chamberlain, located 2 owls in spruce-fir forest. In 1987, a pair of radio-marked owls nested in spruce fir forest. Our observations of breeding owls in spruce-fir forest showed that although some birds roost and forage in spruce-fir while nesting in the abundant cavities of lower mixed conifer or aspen stands, other owls do nest in spruce-fir.

Nest Box Experiment

Although nest sites were not random draws from available habitat we questioned whether nest stands were used because of some structural characteristics or simply due to cavity availability?

Cavity availability was higher in mixed conifer and aspen stands than any other type (pers. obs.). At Chamberlain we never saw a large cavity in lodgepole pine forest. Because Douglas-fir snags rot uniformly from heartwood through sapwood, they also produce low quality cavity substrate. We saw few usable nesting cavities in Douglas-fir or spruce-fir forest.

To test the relationship between cavity availability and forest structure in nest site selection we initiated a small nest box experiment. We hung nest boxes in 3 forest types; 19 in lodgepole pine, 11 in Douglas-fir, 15 in mixed conifer. We also placed 2 in aspen, and 3 in spruce-fir forest.

During 4 years only 4 boxes showed evidence of active courtship or nesting by boreal owls, too small a sample for statistical analysis. Most striking, boreal owls did not use nest boxes in lodgepole pine forest. In 1987, a pair of radio-marked owls courted at a box in aspen but moved 0.5 km to a box in mixed conifer and fledged 2 young. A second box in mixed conifer fledged 2 young in 1988. In 1987, boreal owls nested in a box in Douglas-fir forest but the young died at 14-18 days old.

Nest Tree Characteristics

During intensive studies in the RNRW we found 23 boreal owl nests; 22 at Chamberlain and 1 at Cold Meadows. Locating nests other than those used by radio-marked females was difficult. We found 6 nests when neither the male nor the female was marked, 4 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 all but one natural nest cavity to pileated woodpeckers; northern flickers probably excavated the other. Cavities excavated by pileated woodpeckers were oval with a larger vertical dimension than horizontal. Boreal owl nest cavity entrances averaged 102 mm ± 12.41 mm diam high (range 64-150 mm) and 95 ± 11.89 mm diam 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. The interior of several cavities had rotted to the extent that the cavity base was not flat. In these cases, recesses 3 to 5 cm deep along the edges of the base extended into the rotting wood. Inside, the cavities ranged from 7-50 cm deep ($\bar{x}$= 31 ± 7.61 cm) and from 15-26 cm diam ($\bar{x}$ = 19 ± 2.11 cm). The incubating owl could look horizontally out of the nest entrance at one nest. The tree diam at the cavity averaged 41 ± 5.21 cm (range 26-61 cm). Tree diam at breast height averaged 64 ± 11.02 cm (range 33-112 cm).

Excluding the 4 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, one aspen, and one Douglas-fir. Snag condition included 3 old branchless stubs, 2 hard snags with sloughing bark and only large branches remaining, and 5 young snags with bark and complete limbs. For nests in live trees, all but 2 cavities occurred in an open area on the tree bole. For live trees (n = 8) the distance to foliage above the cavity averaged 3.8 ± 1.67 m (minimum 0.3 m). Over 3 quarters of the cavities in live trees had no foliage below the cavity. For those which did, the minimum distance to foliage below was 0.6 m.

The owls chose relatively high cavities, averaging 12.7 ± 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 one of the uppermost cavities suggesting a preference for high nest sites. Cavity entrances faced all cardinal directions in nearly equal proportions.

The forest immediately around nest trees had an open structure. Density of 2-23 cm dbh trees within a 0.01 ha plot around the nest tree averaged 398 ± 162 per ha (range 0-1482) (Table 5). The density was 3 times lower than the average at winter roost sites. Density of trees larger than 23 cm dbh averaged 212 ± 86 per ha, similar to average densities measured at winter roost sites. All nests faced a forest opening at least 5 m diam immediately in front of the cavity allowing a clear flight path to the nest.

To rigorously test whether tree density was significantly less immediately around the nest tree we compared measurements in a 0.01 ha plot around the nest to a 0.03 ha "donut" surrounding this inner plot. Density of 2-23 cm dbh trees was slightly less near the nest (mean difference -- 144 trees/ha), but our sample was not sufficient to demonstrate a significant difference (paired T-test t=-1.88, df=22, _P_=0.0735). Likewise, there was no difference in the number of large trees (> 23 cm dbh) near the nest compared to the surrounding circle (_P_ = 0.57).

Nest sites occupied forest stands in 3 habitat type series. We found 17% of nest sites in Engelmann spruce (_Picea_ _engelmannii_/_Equisetum_ _arvense_) habitat types, 39% in subalpine fir habitat types including _Streptopus_ _amplexifolius_, _Calamagrostis_ _canadensis_, _Xerophyllun_ _tenax_, and _Vaccinium_ _scoparium_ series, and 44% in Douglas fir habitat types including _Symphoricarpos_ _albus_, _Calamagrostis_ _rubescens_, and _Carex_ _geyeri_ series. The slope at the nest ranged from flat to 49%, averaging 28% ± 5.87%. Nest trees were distributed relatively evenly from bottoms to upper slope positions (27% bottoms, 18% lower-third, 14% mid-third, 41% upper-third). We failed to locate any nests on ridges.

Roost Habitat and Roosting Behavior

Unlike many species of owl, boreal owls roost at sites scattered throughout their home range; rarely do they roost in the same stand on consecutive nights. The owls seldom use the same roost tree more than twice in a given year. At fewer than 10 of 882 roost trees did we find more than 2 fresh pellets. From 1984-1986 we located consecutive daytime roosts of 12 owls on 94 occasions. These locations gave an indication of the dispersion of roost sites. Treating each of the 12 owls as samples and consecutive roost locations for an individual as subsamples, the average distance between winter roosts was 1460 ± 433m and in summer 868 ± 483m (Hayward et al. 1987b).

Our observations suggest that boreal owls roost in a tree near the end of their last foraging bout each morning. Roost selection, then, involves choosing a site from the range of those available when foraging ceases. Foraging and roosting habitat selection, therefore, are not independent in that roost macrohabitat characteristics will be dictated largely by selection of foraging site. In the following discussion we will concentrate largely on microhabitat structure at the roost, leaving an extended discussion of macrohabitat to the section on foraging.

Pattern of Roost Habitat Use, Winter and Summer.--As a result of shifts in home range use between winter and summer, the habitat type of roost stands differed between seasons ($\chi^2 = 167.63$, df = 7, $\underline{P} < 0.001$) (Table 6). These differences reflect the use of more moist, higher elevations in summer. The topographic position of roost sites also differed between seasons ($\chi^2 = 63.73$, df = 6, $\underline{P} < 0.001$). Boreal owls roosted in bottoms significantly more often in winter (27% vs. 9%) and on mid - and upper-slopes significantly more often in summer (12% vs. 26% mid slopes, 29% vs. 41% upper slopes, for winter vs. summer).

Typical forest stands used for winter roosts had nearly 60% canopy cover, 26 m^2 per ha basal area, 1620 trees per ha 2.5-23 cm dbh, and 165 trees per ha over 23 cm dbh (Table 7). Although similar to winter roosts, summer roosts, on average, appeared to be in denser forest with greater cover. The univariate measures of forest characteristics (Table 7) suggest that winter and summer roost sites differed. Do boreal owls choose forest with different structure in winter and summer?

We measured habitat structure at numerous roost sites for each of 24 radio marked owls. Thus, the 424 roosts we measured were not completely independent. Therefore, to test for differences across seasons we cast a 2 way MANOVA blocking by individual owl. Through this analysis we controlled for the effect of individuals and we could test for interactions among seasons and owls.

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. Winter roosts were in stands with fewer sapling and pole trees than summer roosts. A canonical analysis run to clarify the results of the MANOVA indicated that basal area and canopy height at roosts differed least between seasons; canopy cover and large trees (> 23 cm dbh) were moderately associated with seasonal differences; and small trees (2.5-23 cm dbh) were most strongly responsible for the seasonal difference in roost structure.

Individual boreal owls also differed significantly in roost habitat (MANOVA Wilks' F = 2.34; df = 154,2544; P = 0.0001) although the small F value indicated the effect was much weaker than the difference in seasons. Individual owls differed most in the density of large trees, canopy height, and basal area. The effects of individual owl and 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 straight forward. As we will show later, owls shifted home range slightly between winter and summer. The differences between seasons in roost habitat structure, then, 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 looked for seasonal differences in the *random* sites measured in conjunction with the owl roost sites. As explained in the methods, we measured vegetation on random sites paired with each roost. Therefore any difference in microhabitat resulting from seasonal shifts in home range should also be apparent in the random plots. The random plots, then, act as a control for the confounding variable, home range shift.

We, again cast a MANOVA, blocking by owl, to test the season effect and interaction. The results support the assertion that owl roost habitat differs between summer and winter. No season effect (MANOVA Wilks' F=1.63; df=7,198; P=.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 = 133,1318; P = 0.0001) but was rather weak judging by the relatively unsatisfying F value. The large number of degrees of freedom in this analysis suggest good power to detect even small differences in season, so we are confident with our conclusion that random plots showed no seasonal effect.

Roost Perch Characteristics.--During winter (N=261) boreal owls typically perched 7.18±0.21 m high in a 27 ± 0.94 cm dbh tree. 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 ± 0.15 m, distance to foliage below averaged 0.7 ± 0.15 m, and distance to foliage at the side averaged 0.3 ± 0.06 m.

In summer (N=378) boreal owls continued to roost in the dominant tree species of the stand (66% of roosts were in dominant tree species). Birds perched at a mean height of 5.89±0.16 m in 25 ± 0.69 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 ± 0.14 m above the owl, 0.7 ± 0.10 m below, and 0.4 ± 0.06 m to the sides.

Roost Habitat Selection.--Do boreal owls choose roost sites or simply roost in any available tree? Based on our observations of 882 roosts we saw little pattern in winter roost selection but felt boreal owls selected cooler microsites during summer. During hot weather the birds roosted in a large dense tree or a tree in a dense patch of timber. When we compared the difference in temperature at the roost and in the nearest opening (both temperatures taken in shade) we found a significant difference for temperatures above 40^{o} F. The difference in temperatures increased with increasing temperature (Table 8).

When we compared measurements of forest structure at roost sites and paired random sites some interesting characteristics became apparent that reinforced our observations. In both winter and summer, roost sites differed significantly from paired random sites but summer roosts showed more pronounced differences. The Hotelling's T^2 statistic for winter was marginally significant at $\underline{P} = 0.021$ (F = 2.04; df = 120,106); for summer it was highly significant ($\underline{P} < 0.0001$, F = 3.75; df = 120,106). These results suggest that during summer the owls chose roosts with stand structure different from that available in the immediate vicinity. In winter the tendency to do so was weaker.

Looking at individual characteristics of forest structure, winter roosts had significantly greater canopy cover, more 23-38 cm dbh snags in the 0.008 ha plot, and fewer 15-23 cm dbh snags than random sites ($\underline{P} < 0.05$). Summer roosts had greater canopy cover, higher basal area, denser 2.5-15 cm dbh trees in the 0.008 ha plot, and denser 23-38 cm trees in both the 0.008 and 0.04 ha plots ($\underline{P} < 0.05$) than random sites.

Observations of 2 owls whose summer home ranges included extensive even-age lodgepole pine forest with small patches of mature, uneven age spruce-fir further demonstrated the owls' choice of particular forest sites which provide moderate microclimate (or temperature). In 1987, a female who nested successfully moved 15 km in 6 days 2 weeks after her young fledged. For at least the next 2 months, she used a relatively small area (ca 300 ha) of forest at 2200 m elevation (305 m above her nest site). The forest within this summer home range was dominated by lodgepole pine but the owl invariably roosted in small (ca. 2 ha) stands of spruce-fir or Douglas-fir. By the following February, however, she had returned to the vicinity of her earlier, lower elevation nest site. Other owls exhibited similar behavior (B117, B043). These results show that, especially during summer, boreal owls seek forest with particular structural characteristics to roost. Is there any evidence that they also choose particular perch characteristics?

<u>Perch Selection</u>.--Boreal owls perched within 15 cm of the bole of the tree 72% of the time in winter and 77% in summer. Such strong selection for roost position suggests that the bole of the tree provides security from enemies or aids in thermoregulation. Does the roost tree aid the owl in thermoregulation?

We examined the influence of several climatic and weather variables on the choice of roost position. We reasoned that the aspect of the roost perch from the tree bole should depend on wind direction, wind speed, air temperature, and season of year, if behaviors related to thermoregulation were most important in roost perch selection. Thermoregulatory stress, however, is not a constant factor but may only be important under extreme weather conditions. Thus, defining the importance of thermoregulation in determining roost perch selection is not possible without experimentation. The observations described below can only suggest in a gross way whether thermoregulation influences perch choice.

During winter the distribution of perch aspects (measuring aspect of perch from bole of tree) was not uniform (χ^2 = 19.708, df = 3, $\underline{P}$ = 0.0002). The owls perched most often in the southern quadrant and seldom in the north quadrant (cell X^2, $\underline{P}$ = 0.0005, $\underline{P}$ = 0.013, respectively). The direction of the wind at roosts also was not uniform (χ^2 = 14.11, df = 3, $\underline{P}$ = 0.0276) but blew most often from the north which could account for the nonuniform distribution of roosts. A test of the relationship of owl aspect to wind aspect was not significant ($\underline{P}$ = 0.389) suggesting that on the whole wind direction did not account for the predominant southern exposure of winter roost perches. Perhaps increased insolation on the south side of the tree was more important.

The degree to which the tree sheltered the owl from the wind did not interact with wind speed (χ^2 = 14.69, df = 12, $\underline{P}$ = 0.25) indicating that owls in winter did not have a stronger tendency to sit on the leeward side of the tree when wind speeds were higher. There was, however, an interaction between the temperature at the roost and the tendency for the owl to use the tree to block the wind (χ^2 = 20.26, df = 9, $\underline{P}$ = 0.016). Most important, at temperatures below 25° F, owls sat on the sheltered side of the tree where as at higher temperatures they frequently perched so that the tree provided little shelter. We hasten to add that this pattern was not strong and the interaction of temperature and perch position was not easily interpreted. The difficulties encountered interpreting the one way interactions (i.e. difference in wind and perch aspect vs. wind speed, perch aspect vs. temperature etc.) likely arise because several weather variables may simultaneously influence choice of roost in addition to factors related to concealment from predators.

During summer the owls showed no tendency to perch on a particular aspect of the bole ($\underline{P}$=0.11). Summer wind directions were uniformly distributed in compass direction (P = 0.355). Unlike winter, roost aspect did appear to be influenced by wind direction. Perch aspect and wind direction were strongly related ($\chi^2 = 40.85$, df = 9, $\underline{P} < 0.001$); owls most frequently perched on the leeward side of the bole. Wind speed and air temperature did not significantly influence tendency for owls to sit on windward or leeward sides of the tree.

We used regression analysis to further test the influence of wind speed and air temperature on the difference in roost and wind aspects. For both winter and summer a multiple regression was far from significant (winter $\underline{P} = 0.65$, summer $\underline{P} = 0.46$). None of the independent variables had a partial regression coefficient with a $\underline{P}$ value less than 0.21.

The consistency displayed by boreal owls in choosing roost perches adjacent to the tree bole, as discussed above, suggests active selection by the owls. Selection of perch conditions, however, involves far more than deciding how close and on which side of the bole to perch. We also sought to explore the owl's choice of cover immediately above, below, and to the sides of the roost perch. By perching either high in the crown of a conifer or below the foliage, or in a witch's broom, an owl can control the amount of protection the roost affords from enemies or the weather. What was the pattern of perch choice by boreal owls at Chamberlain and could the pattern, if any, be explained as behavior related to weather conditions?

We rated the density and extent of cover above, below, and to the sides of owls located on their daytime roosts. For each of the 3 directions, we assigned a rating from 1 (no cover) to 5 (dense cover). During both winter and summer sometimes we found owls roosting on open perches with no cover within 2 meters or more, and on other occasions roosting in witch's brooms, under large branches, or surrounded by dense foliage. The owls consistently sought dense cover above the perch during rain but tolerated snowfall. We frequently observed owls move to a shaded perch on hot summer days when the sun shone on the roost. In contrast, on other occasions we watched owls sit in sunshine for over an hr in both winter and summer. Especially during autumn, when temperatures were in the 40° F range, owls frequently sat in the sun for periods over an hr with their eyes closed. We also observed owls roosting in dense cover during clear, calm, warm weather in winter and summer. The pattern of cover density at daytime roosts, then, was not obviously related to weather. In short, we saw no clear relationship between roost cover and weather.

To explore the relationship between cover at the roost and weather more carefully we examined frequency tables relating cover vs. temperature, cover vs. wind speed, cover vs. the difference in perch aspect and wind aspect, and cover vs season. Chi-square analysis revealed no significant relationships despite large samples (N=608 roosts).

The contingency table analysis did not permit us to look at the influence of several weather variables, on cover density, on all sides of the perch, simultaneously. Therefore, we cast a MANOVA testing the main effects of air temperature, wind speed, difference in bird aspect and wind aspect, and season without interaction terms. Dependent variables included cover ratings above and below the perch and the sum of cover ratings above, below, and to the sides.

Air temperature at the roost was the only significant effect on cover density (MANOVA Wilks' F = 2.89; df = 3,454; $\underline{P}$ = 0.036) This F value isn't extremely satisfying. The high degrees of freedom suggest that even a small effect due to temperature could be detected. Examining plots and frequency tables of air temperature vs. cover rating revealed no biologically interesting pattern. The effects of wind speed, season, and difference in wind aspect and perch aspect were all far from significant (minimum $\underline{P}$ value > 0.40).

Roosting Behavior.--Daytime is a period of reduced activity for boreal owls. During daylight the owls spend the majority of time perched, eyes closed, often with the bill tucked under a wing or nestled in the breast feathers. 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 min before being interrupted by brief (2-5 min) periods of preening or actively looking about. Gusts of wind frequently "awakened" the owls leading to preening. The owls spent 6% of the observation period preening. The birds preened plumage and feet, pulled vigorously at the transmitter harness, stretched wings, and on some occasions shook the entire plumage. Except for the extended preening bout of 20-30 min 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 one roost perch to another (1%) encompassed only a short portion of the daytime activity but may be important. Owls were observed gullar fluttering during 1% of the 46 hrs of observation.

Boreal owls frequently consume 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.

Boreal owls tended to eat or possess cached prey more frequently in summer than winter (χ^2=56, df=1, n=822, P=0.00001). We observed owls with cached prey on 17% of summer roosts and 4% of winter roosts, a significant difference in proportions ($Z = 4.52$, $P < 0.00001$). During summer the owls eat cached prey most frequently between 1200 and 1400 h; 65% of observations of owls consuming cached prey occurred between 1120 and 1330 h. In winter we observed boreal owls eating prey throughout the day although a third occurred before noon. The distribution of feeding times differed from the distribution of our roost location times for both winter and summer (winter $\chi^2 = 6.317$, df = 3, $P = 0.097$; summer $\chi^2 = 7.662$, 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). The marginal significance, however, does suggest that the owls do not show strong preference to feed at particular times of day.

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 piecemeal. They frequently consumed the prey while perched on a limb larger than a typical roost perch branch (2-4 cm diam) or on a spreading, foliated bow of fir or spruce. They held the prey against the perch with one foot while picking at the prey with the bill. 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 generally consumed whole.

Our method of recapturing owls at their roost demonstrates that they will attack prey during day. We recaptured owls on 17 occasions using a mist net and a tethered mouse. The owl flew toward the prey and was captured in the mist net just prior to contact with the mouse. The owls do not, however, always take advantage of prey available at the roost. Boreal owls failed to attack tethered mice as often as they did attack. On some occasions, boreal owls also took no notice of wild (unrestrained) chipmunks (Tamias amoenus), mice, and voles at the roost. We observed owls attack prey from their roost (excluding instances of extended daytime foraging) on 7 occasions from 639 roost observations.

Boreal owls seldom forage for an extended period during daylight. On only one of 16 days (46 hrs) when we watched roosting owls for over 2 hrs at their roost, did an owl begin hunting. The owl foraged for 15 min No active foraging, including flights, rapid head turning and other foraging behavior, was seen on the other 15 days. 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 0.5 to 1 hr observation period at the roost.

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.

While roosting the owls showed a variety of behavior in response to other animals in the area. We never observed the owls in the presence of mustelids although we observed fresh marten tracks beneath roosting owls. Boreal owls showed little concern at the approach of deer or elk. When we approached the owls they rarely showed more concern than watching us wide-eyed unless we moved within 2 m of the bird. Often the owls only opened their eyes slightly when we first approached and slept during the hr we collected data on the roost. Twice we recaptured boreal owls by hand, indicating their reluctance to move even when approached closely.

Boreal owls show little reaction to mobbing by passerines. Kinglets (Regulus satrapa), chickadees (Parus gambeli), juncoes (Junco hyemalis), nuthatches (Sitta canadensis), thrush (Catharus spp.), or pine grosbeaks (Pinicola enucleator) mobbed roosting owls during 17 of our roost visits. Most often the owls watched the mobbing birds with "casual" slow head movements, and in some instances the owls sat with eyes closed. Boreal owls responded more dramatically to gray jays (Perisoreus canadensis) or Clark's nutcrackers (Nucifraga columbiana). The owls never attacked the intruder but watched jays and nutcrackers more closely or moved to sit on and protect cached prey. On 2 occasions as jays approached, the owl moved to a cached prey and consumed it more rapidly than usual. Frequently, before we would note an approaching flock of jays the owl would become alert. The calls of jays in the area would elicit the same response. In response to the flight of a raven (Corvus corax), hawk, or falcon above the tree tops, the owls always assumed a rigid, contracted "concealing" posture.

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 7 occasions (N=121). One pair was found roosting together 4 times. Their roost behavior is especially interesting. 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 one another, but this time near 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 one another 3 km from the nest and were together near the nest by 2145 h. This behavior suggests that the owls traveled together during some night-time 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 one another 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

Distance Covered.--Boreal owls lead a very mobile existence during both winter and summer. The birds use large seasonal home ranges and frequently traverse much of the home range in the course of a couple weeks. Although the limitations of travel within the wilderness prevented us from effectively following radio-marked owls during their foraging (Hayward 1987), 2 indices 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 distances traveled by boreal owls during their daily activities. Although both measures certainly underestimate daily movement and the magnitude of the bias is unknown (Laundre et al. 1987), these indices do provide insight into the pattern of owl movements by suggesting minimum distances traversed.

We recorded distances between consecutive daytime roosts of 14 owls (7 females and 7 males) on 150 occasions over 4 years. We feel that daytime roosts of boreal owls occur near the final foraging location from the previous night. Boreal owls observed foraging during daylight chose roosts within 50 m of their final foraging perch. Distance between roosts on consecutive days ranged from 0-6935 m. Mean distances did not differ significantly between winter and summer although there was some tendency for winter roosts to be spaced more widely (winter $\bar{x}$ = 1540 ± 446 m, summer $\bar{x}$ = 934 ± 348 m).

The distance between roosts on consecutive days and general pattern of movements seen in sequential relocations of 22 owls presents a crude picture of how the owls use space on a day to day basis. The owls did not usually concentrate their foraging effort in a restricted portion of their home range for several days. Rather the birds tended to move frequently to new forest stands a km or more apart from day to day (example Fig.3). This pattern of movement--spreading use across the landscape from day to day--was the norm for birds during winter (courtship) or nesting. Only when owls were not nesting did they use a small area intensively, confining their activity to several forest stands. During summer following nesting, B055 in 1986, B076 in 1985 and 1987, and owls B133 and, B117 in 1987, were found repeatedly within several ha ranges using the same forest stand for an extended period. This change in movement pattern from dispersed use with consecutive roosts located in different drainages to a concentration of activity in a confined area appeared to be associated with the end of nesting. During courtship and nesting the owls must travel from a foraging site to the nest one or more times a night to deliver prey. This activity, of course, increases the cost of foraging at distant locations and may present some difficult navigational demands associated with locating former foraging sites. The relative costs of foraging in different stands changes dramatically between courtship-nesting periods and post-nesting and may substantially change day to day movement patterns.

The distance between male owl daytime roosts and their nest also provides some insight on the magnitude of movements during nesting. Our observations (described under Roosting Behavior and Foraging) suggest that roost sites result from selection for foraging habitat and to avoid heat stress during summer. At Chamberlain, nest sites and habitats providing other needs were often not adjacent (Fig. 4-A). Nesting males rarely roosted within 500 m of the nest and over 85% of 72 roosts lay over 1000 m from the nest and up to 5600 m away. There was no tendency for the roost to nest distance to increase or decrease during the course of nesting. The average roost to nest distance of 5 owls over the 4 year study was 1729 ± 831 m.

Nighttime radio-telemetry (triangulation) indicated that the roost to nest distances were accurate estimates of foraging distances. Following prey deliveries at the nest, one owl on 3 nights returned to the area of its daytime roost several km from the nest. Four other males also left the nest stand immediately after prey deliveries to forage in areas distant from the nest.

Foraging.--Boreal owls might be classified as sit and wait predators, or searchers, (as opposed to pursuers) but are very active while hunting. While foraging, a majority of time is spent searching; little time is spent actively pursuing prey. During a foraging bout, the birds move through the forest in an irregular or zig-zag pattern, flying short distances between perches. They spend a majority of time perched. 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 birds' intent, wide-eyed attitude.

Boreal owls at Chamberlain hunted mainly after sundown. As described under Roosting Behavior, daytime-hunting was not common and accounted for less than 1% of the owls' activity. From our observations, we suspect that over 90% of prey are captured after dark.

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. We observed hunting owls on 16 nights and recorded quantitative data on 10 occasions including 5 different owls. These observations spanned 31.25 hrs. After dark, the owl often was seen only intermittently despite our use of night vision goggles and betalights (Hayward 1987). We watched owls hunt during daytime 13 times and recorded quantitative results on 8 days for 4 different owls. Diurnal observations spanned 7.2 hrs. 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 ± 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 under 40 m. In the forest environment we were unable to record long flights and therefore our sample has a negative bias. We feel this bias influenced the observations only slightly. In virtually all situations, we could observe flights up to 30 m. 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.

Prior to detecting prey the owls seldom flew less than 10 m between perches. When prey was detected, the owls rarely attacked immediately. Rather, they moved closer with several short flights of 1-5 m. These short flights apparently are not a stalking pursuit but an effort to determine the location of prey. The owls will attack voles from 20 m when the prey is visible.

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.

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 less than 5 min, 64% for less than 3 min, and 27% for one min or less. Four percent of hunting perches were used more than 10 min If an owl used a perch for more than 10 min, it either ceased foraging or was intently listening to a potential prey. One owl observed hunting at night watched a witch's broom clump in a lodgepole for nearly 12 min prior to flying 2 m into the witch's broom after a roosting passerine. Another owl hunting during daylight flew approximately 4 m to catch a redback vole (Clethrionomys gapperi) deep in a clump of beargrass after watching the spot for 10 min.

Not all attacks are preceded by an extended vigil. The owls seem intent on waiting for prey to move to a vulnerable position or until they are certain of the prey's location but will attack immediately after prey is detected if it is vulnerable. We witnessed an owl make 3 attacks on different prey in 20 min; 2 were successful. The owl apparently initiated 2 of these attacks within a min of detecting the prey.

While searching for prey, boreal owls perch on relatively low branches. Perches during foraging observations averaged 4 ± 0.6 m high. Seventy-five percent of 114 perches were less than 5.5 m. Perches ranged from 0.5 to 9 m. Owls used perches less than 1.5 m almost exclusively after prey was detected. After hearing a potential prey, the birds sometimes moved toward the sound in short flights moving to lower perches. For example, on 7 July, a male spent 16 min moving toward an unsuccessful attack on a ground nesting junco (Junco hyemalis). It changed perches 6 times, dropping from 4 m to approximately 0.4 m before attacking. Although we recorded few attack distances, the usual attack flight seemed about half the distance of flights between hunting perches.

Seasonal Movements

Both changes in weather conditions through the year and stage in breeding chronology influenced movement patterns of the boreal owls at Chamberlain. Because boreal owls are not migratory, some changes in movements through the year were rather subtle and likely result from the particular geographic characteristics of Chamberlain Basin. Other seasonal movements appeared to be independent of characteristics of the basin.

The most obvious shift in movement between winter and summer was the use of higher elevation roost sites during the snow free period. Each of 12 owls radio-marked during winter and summer exhibited some shift in the elevation of their average seasonal roosts. Three owls (2 males and a female) used roosts during summer which averaged over 335 m higher than winter roosts. The difference between elevations of summer and winter roosts of 12 owls averaged 186 ± 105 m.

Although the owls demonstrated a consistent tendency to use higher elevations in summer, overlap between seasons was complete. During winter owls spent some time in the highest portions of the study area despite snow depths of 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 birds spent in each elevation zone.

The timing of shifts from low to higher elevations from winter to summer was not related to breeding chronology. The shift coincided more with rising daytime temperatures. Both mated and unmated males shifted to higher elevation roosts in May and June even though mated individuals supported nesting females at low elevations.

Following the shift to higher elevation roosts in spring, the necessity for mated males to visit the nest site resulted in longer daily movements for these individuals than other owls during spring and early summer. Unmated owls became sedentary compared to mated owls during summer. Two unmated males we observed (1 was followed for 2 yrs) frequently moved only 100-200 m between consecutive roost locations and remained within several forest stands for most of the summer.

Seasonal movements associated with nesting chronology were dramatic for some females. During winter, we noted no obvious difference in the movements of males and females. With the onset of nesting, of course, females were confined to the nest cavity except for short flights from the nest to defecate, regurgitate a pellet, and remove debris from the nest. When the young reached about 20 days of age, females ceased occupying the cavity. Females differed considerably in behavior upon leaving the nest. We monitored radio-marked females from 6 nests. 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 home ranges similar to their pre-nesting ranges 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 a small area which she occupied for at least the next 2 mo. 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. She remained in this area until 27 September when she moved to lower elevations near the nest.

Year to Year Movements

Movements of radio-marked owls provide some indication of the degree of site tenacity in the Chamberlain Basin population. We gathered evidence suggesting owls at Chamberlain exhibit both year to year site tenacity and nomadic emigration. We observed male and female boreal owls who stayed in the basin for more than one year and used the same home range. We also documented emigration of adults from the population.

In late summer or autumn 1984-1987, we placed fresh radios on 4, 5, 2, and 5 owls, respectively, in an effort to relocate the birds during the following winter (4 mo later). Of 16 owls, 8 were relocated when we returned to the study area. Two other radio-marked owls were each recaptured 2 yr after their initial capture. Whether the remaining birds emigrated, died, or the transmitters failed can not be determined. Despite searches from aircraft, no signal was located from the 4 birds marked in 1984. We suspect radio failure for at least some radios that year because 2 adult birds whose radios were not replaced for winter in 1984 were recaptured in subsequent years.

Using evidence from both radio-marked birds and banded individuals, we found 6 males and 4 females which remained in the basin for more than one yr. Six radio-marked males each used portions of their original home range in the second year. For 2 males monitored closely through both winter and summer in 2 yrs ($\geq$20 locations per season), seasonal home ranges from the 2 yrs matched closely. One of the males nested in cavities 1.4 km apart on consecutive yrs.

Unfortunately, our home range information was not as complete for the 4 females which were radio-marked for more than one yr. The degree of home range tenacity among females, therefore, could not be determined.

Each yr we checked nest cavities used by owls in previous yrs (n = 25). Although 2 nest trees were re-occupied we never located an individual female in the same cavity she used previously. Nest sites of 2 individuals were known for 2 yrs. One bird nested with a different mate in 1984 and 1986 in cavities 1.4 km apart. The second female used cavities 7.6 km apart in 1987 and 1988.

In light of the evidence for year-round residency, several observations of emigrating are important. As presented earlier, 2 females emigrated from the Basin 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 emigrating males wore new radio-transmitters. Neither owl was relocated in repeated ground and air searches in the study area. One male (B043) was first captured in 1984 so left the Basin after living there at least 2 yrs. The second male was first captured in 1985. After emigrating, he was relocated on 7 May 1986 80 km to the west near Upper Payette Lake, Valley Co., Idaho.

Home Range

Home Range Area.--We estimated the area used by boreal owls at Chamberlain during winter and summer from radio-marked owls in 1984-1987 (for examples see Fig. 4). For these estimates we used 95% utilization distributions calculated from harmonic mean distances (Samuel et al. 1985). Mean winter home ranges covered 1,451 ± 522 ha for 13 owls (5 females, 8 males) over the 4 year study. Summer ranges generally covered smaller areas; they averaged 1,182 ± 334 ha for 15 owls (4 female, 11 male). Year round ranges averaged 2121 ± 859 ha for 16 owls (4 female, 12 male) (Table 9). These values must be considered minimum utilization distributions. Our sample of each owl's activity was quite small and like all kernel estimators the harmonic mean method is biased low with small samples. See Hayward et al. (1987b) for further discussion of seasonal home range.

Owls did not spread their activity evenly through their home range. During both summer and winter, we identified core areas in the seasonal home ranges. Core areas are portions of the utilization area used more intensively and are identified objectively in the program Home Range (Samuel et al. 1985). During any season most owls concentrated their activity in several areas within the home range (Fig. 4) and explored other areas infrequently. The owls rarely used one area for more than 2 weeks, however, but moved back and forth among intensively used areas. As discussed in Hayward et al. (1987b) evaluation of 55% and 95% utilization distributions also suggests that boreal owls concentrate activity in small portions of the home range.

Home Range Overlap.--We did not analyze overlap in utilization distribution quantitatively. The minimum convex polygon which is usually used for such analysis gives a distorted picture of how similarly 2 owls use space. Extreme overlap in convex polygon estimates can result even when 2 individuals spend little time using the same land base. Unfortunately calculating overlap in utilization distributions is not trivial and has not been incorporated into the program Home Range.

Our observations did show that areas used by boreal owls overlap considerably, regardless of owl sex. Overlap of male home ranges is of greatest interest. In any year, male owls inhabiting the same drainage often used the same forest stands intensively. Overlap of some utilization distributions were nearly complete. Most often the owls did not use a stand at the same time although we found males roosting as close as 200 m. On 2 different nights we captured 2 males at a 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 10). 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). Avian prey included warblers, thrushes, mountain bluebird (Sialia currucoides), crossbill (Loxia curvirostra), dark eyed junco, western tanager (Pirango ludoviciana), gray jay, hairy woodpecker (Picoides villosus), and pine siskin (Carduelis pinus). Some avian remains in pellets and at nests could not be identified. Crickets dominated insect remains. The most surprising prey included a weasel (Mustela spp.) taken by a female in late winter, a young woodrat (Neotoma cinerea) taken by a female owl in summer, and 2 pica (Ochotona princeps) taken by male and female owls.

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. (Biomass estimates were calculated by multiplying prey frequencies by estimated prey weights in Table 11 . Redback voles and pocket gophers (Thomomys talpoides) together accounted for over 65% of estimated biomass of prey, underscoring the limited range of prey important to the owls. Redback voles alone accounted for 35% of individual prey in our sample from winter and summer.

Diets of individual owls differed significantly in both winter and summer (summer $\chi^2 = 55$, df = 25, $P < .01$; winter $\chi^2 = 20$, df = 10, $P = .025$). In our test of heterogeneity among individuals we considered only those owls for whom we recorded 30 or more prey in one season (6 males in summer, 3 males and 1 female in winter). We eliminated the single female for 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. The conclusion that owls differ in diet within a season is confounded, however, because data were collected during several years when prey availability differed.

The major differences in diet among individuals involved unusual numbers of uncommon prey taken by particular owls. While samples from some boreal owls included no avian prey, the diet of one male (B096) included 10% birds during summer (41% of all avian prey taken by 8 males during summer). This same male captured 54% of the chipmunks taken by males during summer. Two other individuals captured inordinate numbers of jumping mice (Zapus princeps) and crickets. Despite these differences, redback voles were the most frequently captured prey for all individuals in both winter and summer.

Given the strong variation in diet among individuals it is difficult to test for differences between sexes, seasons or years. Our sample included few individual owls with large numbers of prey in both winter and summer or in several years. Keeping in mind these sampling problems, however, we can make some statements concerning seasonal prey and dietary differences between sexes without using statistical inference. Several patterns appear quite strong. The evidence for these patterns must simply be regarded as tentative.

Seasonal Prey Use

During winter the owls relied on redback voles for nearly 50% of prey items captured (Table 10). These voles accounted for 38% of the biomass in our winter sample. The range of prey species available in winter is less than summer and is reflected in fewer important species in the winter diet. Pocket gophers, one of the most important summer prey, jumping mice, and chipmunks are all unavailable during the period of winter snow pack. (During early and late winter when snow 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 became extremely important prey accounting for 19% of overall winter prey biomass (7% by frequency) despite the limited period they were available.

Flying squirrels (<u>Glaucomys</u> <u>sabrinus</u>) are the only prey taken considerably more frequently 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. The proportion of female winter diet represented by the flying squirrel may be exaggerated for 2 reasons. These prey are extremely visible when cached at a roost and are not consumed in a single day. Therefore the sample may be biased. This bias, however, would not influence the difference in winter and summer records of flying squirrels which is quite dramatic.

Female owls with flying squirrel prey remained sedentary for a night with the cached prey. This behavior underscores the importance of these large prey for females. After capturing a squirrel an owl had secured food for more than one day and could conserve energy normally expended while foraging during a time of year when prey availability is limited.

During summer redback voles continued to be important in the owl diet; the voles were the most frequent prey and ranked second after pocket gophers in biomass. The owl summer diet broadened compared to winter with the addition of chipmunks, jumping mice and crickets. Crickets may be more important to the 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. In terms of biomass, however, the contribution of insects to the diet is likely not important.

Differences Between Sexes

Our sample of prey from winter and summer over 5 years showed few striking differences in diets of males and females (Table 10). In general female owls did not consume more large prey than males. Females took proportionally fewer chipmunks and slightly more pocket gophers, the 2 most common large prey. Females consumed proportionally more insects, the smallest prey type. The exception to the pattern of both sexes capturing similar size prey concerned prey which matched the owls in size. Our sample of 716 prey captured by male owls included only one adult flying squirrel while over 6% of the female diet was adult squirrels. Likewise females captured the only weasels and woodrats in the sample.

Yearly Variation

As discussed below under Prey Populations, the abundance of certain prey populations changed from 1984-1987 with a low in 1986. Breeding activity of boreal owls in our sample declined in 1985 and reached a low in 1986. Unfortunately, problems in our sample of owl diet precluded objectively testing for changes in diet between years and making statements of statistical confidence. Rather, we must discuss patterns in the data mindful that trends may simply reflect diets of individual owls rather than patterns in the entire population.

In our analysis of yearly variation in diet we have excluded insect prey. Prior to 1986 we seldom recovered pellets at roosts on the day they were cast. Therefore pellets composed completely of insects, which disintegrate quickly, were less likely to be found in the early years of study. Therefore our sample of insect prey was not constant between years.

The frequency of redback voles in prey samples was lower in 1986, the year of poor owl breeding, than in other years. In 1986, 26% of prey were redback 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 importance in 1986 compared with other years. The frequency of Microtus sp. remained relatively constant from 1984-1987 averaging 11%. The importance of the other common prey, shrews and birds, also remained relatively constant.

OWL POPULATION CHARACTERISTICS

Trends In Abundance of Boreal Owls

During the study we recorded data which 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. Little faith can be placed in any single index. In addition, the indices we use are not all independent. If the indices together reveal a coherent pattern, however, we feel they represent substantial evidence that the pattern is real.

Night-time surveys using playback of taped boreal owl calls during each winter suggest a trend in breeding population abundance from 1984-1987 at Chamberlain and 1984-1986 at Cold Meadows (Tables 12, 13). At Chamberlain, 2 related indices show a slight decline in 1985 followed by a substantial decrease in breeding activity in 1986. The proportion of survey nights that we heard boreal owls differed significantly between years (X2 = 20.2, df = 3, p < 0.0001). The low number of successful nights in 1986 contributed most to the difference (cell X2 = 8.54, p = 0.0035). If instead, we look at the number of male owls heard singing per mile surveyed, the same pattern is seen--owl calling rate dropped from a high in 1984 to a low in 1986 with a substantial recovery in 1987 (Table 12). 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 re-surveyed.

Survey results at Cold Meadows showed a similar trend. The proportion of survey nights that we heard boreal owls was twice as large in 1984 as in 1985 or 1986, but due to a small sample the difference was not significant ($\chi^2 = 2.65$, df = 2, $\underline{P} = 0.265$). The ratio of number of calling males heard per survey mile was significantly higher in 1984 (Table 13) than in either of the following years.

The trend of decreasing breeding populations of boreal owls from 1984-1986 before rebounding in 1987, as described above, was also reflected in our winter trapping success at Chamberlain. We captured 9 boreal owls in 1984, 5 boreal owls in 1985, 3 boreal owls in 1986, and 7 boreal owls in 1987. Trapping effort for each year is difficult to quantify because our trapping strategy differed between years. The number of nights we trapped at sites where we had little confidence of capturing an owl differed between years. Using the number of trapping nights as an imperfect measure of effort, catch/effort during winter equalled 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 one forest stand on different surveys to one 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 miles surveyed. Territories located per mile surveyed equalled 0.35 in 1984, 0.13 in 1985, 0.02 in 1986 and 0.14 in 1987.

Trend in Productivity

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

In all but 2 cases, we observed the clutch size during incubation or at hatching so technically we can only estimate minimum clutch size. From 1984-1987 boreal owl clutches ranged from 2-4 eggs and averaged 3.3, 2.5, 2.5, and 3.5 eggs for each year 1984-1987, respectively. Only 2 nests during this period fledged 3 young, one nest in 1984 and one nest in 1987; for the remaining nests those which fledged young each produced 2 owlets. Clutch size and fledging rate, then, both indicated 1984 and 1987 were more productive than the intervening 2 years.

Although clutch size and the number of young fledged per successful nest were higher in 1984 and 1987, complete nest failure appears to contribute most to variation in productivity. Nests failed due to parental abandonment, predation on the nest, and death of an adult. The pattern of nest failure across years appeared to follow the other measures of breeding activity (calling) and productivity. From 1984-1987, nest histories included complete success of 3 nests in 1984, abandonment of one 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 trend in productivity. In years when other measures of productivity were low, nests failed due to abandonment, especially early in the nesting cycle. In good years, few nests failed: predation was responsible for those nests which were lost.

The only nest which failed in 1985 (a poor year) failed at hatching. We inadvertently disturbed the nest the day the second egg was hatching, having thought the young had hatched several days before. The ultimate cause of abandonment, however, appeared to be the low rate of prey delivery by the male during incubation. During the 2 weeks prior to abandonment prey delivery rate (as measured by an event recorder at the nest) was lower than the average for successful nests during this phase of nesting in other years.

In 1986, 2 undisturbed nests were abandoned early in the cavity occupancy stage; one after 2 eggs were laid, the other prior to laying. For the third nest, the radio-marked male abandoned the nest during a 4-day cold snowy period when the oldest owlet was 18 days old. The female left the nest 2 days later and only fed the nestlings on 2 nights thereafter.

In 1987, the year with the highest breeding activity by all other measurements, nest failure was high. Five of 7 nests which were initiated failed to produce young. One clutch of eggs was preyed upon, possibly by a squirrel long before hatching. Two other nests appeared to be preyed upon midway between hatching and fledging. In both cases, the nest was checked 5-7 days prior to nest abandonment and the oldest of 3 nestlings was about 9 days old in one nest and 16 days old in the other. The young were healthy and developing normally. When the nest was reexamined no sign of the nestlings--bones, feet, bills, could be found in either.

A fourth nest in 1987 was lost when the female was killed, apparently by another raptor, 3 nights after she was first found occupying a cavity for nesting. Each of 3 nights, from the day she was seen in a cavity until we found her radio and a few feathers, there was snowfall and wind. The poor weather may have hampered her mate in providing prey, forcing her to hunt. The fifth failed nest in 1987 was abandoned prior to egg laying. In an attempt to attach an event recorder to the cavity prior to nesting we disturbed the female who abandoned the site and within 8 days occupied a cavity 4.3 km away with a new male.

Mortality and Age Structure

From 1984-1988 we monitored 23 adult boreal owls from late January through August during field studies at Chamberlain as described under Methods. 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 one 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 can not be assessed with our data. The longevity we witnessed in several marked owls suggests that the impact is not severe.

One male and one female wore radio-tags for 916 and 824 days and were still alive at the end of the monitoring period. More important, 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, weight showed no trend. These results suggest that the radio transmitters did not prevent the owls from maintaining normal physical condition. Whether the owls were forced to actively forage for longer periods, exposing themselves to predation can not be addressed.

During the study, 6 owls, 3 males and 3 females, died. Two owls which died during winter (a male and a female) appeared to have starved as 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. Finally, a male died of unknown causes.

A minimum of 5 marked owls, 2 males and 3 females, were lost from the population through emigration. In 3 cases, we monitored the owls as they left the basin, one was relocated 90 km west, near Upper Payette Lake, Valley County, Idaho. Behavior prior to loss of contact led us to conclude that 2 other owls emigrated.

We lost contact with 8 other owls during the August-January periods when we were not at Chamberlain. Each bird had been re-radioed in autumn (4 in 1984, 2 in 1985, 1 each in 1986 and 1987) for continued study the next January. The fate of these birds was unknown as their radios may have failed, they may have died, or they may have emigrated.

We used information from the radio-marked owls to estimate survival of adult boreal owls at Chamberlain (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 bounds, therefore only estimates for the entire study period will be considered. Below we present results of 2 analyses based on different assumptions concerning emigration.

Survival Rate: Analysis A.--Because we monitored owls from mid-winter through summer in most years, estimates of survival restricted to this period are most legitimate. Our first analysis, then, treats only the fate of owls during this monitoring period. For instance, an owl which 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 which emigrate rarely are recruited to a new population. If we assume that all birds which 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 owls during our investigation. Under these assumptions, finite survival from mid-winter through summer expressed as a yearly rate averaged 20% (95% bound 7 to 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 mid-winter through summer expressed as a yearly rate averaged 46% (95% bound 23 to 91%).

<u>Survival Rate: Analysis B</u>.--Analysis A can only apply to owl survival from mid-winter through summer because it only uses radio telemetry results during our field season. If adult survival is similar during autumn and early winter (the period we did not monitor boreal owls) then the above estimates apply for the entire period 1984-1988.

We sought to gather information on autumn-winter survival by remarking owls each fall and searching for them when we returned in mid-winter. We suspect that radio transmitter failure confounded our results but can not determine how many radios failed.

A conservative estimate of year long survival is obtained by assuming that no radios failed and, therefore, any radio not located represented a loss from the population. This analysis yields an average year round survival rate of .317 (95% bound .180 to .946). This result is not satisfying because of the extreme bound on the estimate. Thus, including the autumn and winter in an estimate of yearly survival results in a slightly higher (but not significantly different) estimate with a much broader confidence interval. This result suggests that fall survival is similar or only slightly higher than survival the rest of the year. Results from analysis A, however, yield answers which may apply reasonably well for the entire year.

Breeding Biology

Breeding Chronology: Courtship.--At Chamberlain, some male boreal owls begin 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 out in both cases. The calling rate, measured as the number of owls heard per survey night, increased from January through March. Variation in calling rate through the winter, effects of weather on calling, and pattern of calling during the night will be discussed elsewhere (Hayward, in prep).

Female owls were observed at male calling sites early in the courtship period. In 1984, we captured a female at a calling site while a male called nearby on 5 February. 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 in the study area), 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 pair associate with one another mainly during night-time rendezvous at the potential nest site. As described under Roosting Behavior, members of radio-marked, mated pairs rarely roosted together during daytime. Although we did not explicitly study courtship and, therefore, did not monitor courting owls constantly through the night, our observations of one radio-marked pair suggest that they did not rendezvous at the nest every night during courtship. In 1987, a mated pair which had been courting for at least 2 weeks may have failed to court for 3 nights in succession in early March. The female remained within a km of the nest but appeared sedentary. She had killed at least one flying squirrel, a large prey, and stayed in the vicinity of this cache. By late

March (20-31), the pair appeared to meet nightly in the nest stand. We observed the owls together on all 5 nights which we checked.

The nest of another pair (B085, B086) was observed for the first 6 hrs after sunset 2 nights in succession 2 weeks prior to egg laying. On the first night between 1900 and 0120 hr the male, who was not radio-marked, visited the nest site at least 3 times (2252, 0005 and 0010 hr) singing from perches near the cavity. The radio-marked female never came to the nest stand. The second night (29 April), the female flew to the cavity at 2010 h and the male called by 2030. Again at 2110 h, the pair met at the cavity.

Although the owls often rendezvoused in the nest stand within 2 hours of dark, they met at any time through the night. On 5 April 1987, a marked female was peeping loudly in her future nest stand at 2117 hr. During the next half hour she flew to several cavities within the stand. The male arrived at the site between 2400 and 0100 hr. Two nights later both owls arrived at the nest cavity by 2030 hr.

Our observations suggest that at night during the courtship period male boreal owls sing most often within 200 m of a selected nest cavity, the most common exception being unmated owls early in the courtship period. During observations at nests of 4 radio-marked males on 14 nights, the birds were never heard calling further than 200 m from the nest site. Often the male sings from a tree adjacent to the nest tree or from inside the nest cavity. These observations were not sufficient to determine if the males were singing at sites out of earshot of the nest stand. Other observations do suggest that early in the courtship period unmated owls call from several widely dispersed locations and that the owls visit stands where other males are singing. Even dispersed singing locations all turned out 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 one site. One of the owls nested in the stand that year while one of the others moved about 6 km before the nesting season. In 1985, on 18 February, we captured 2 males when we played the courtship call at one site. One of these owls (B077) nested in a stand 1.6 km from the capture site and the other did not appear to nest. The capture site had been used for nesting the previous year by a different male. Finally, on 31 March 1985, a male (B084) was captured and radio-tagged in the stand used by B077 for nesting that year. B084 was heard calling in the stand on 7 April but he failed to breed that year. On 24 March when we played a tape recorded boreal song at a calling site, 4 radio-marked owls, including the pair which nested at that site moved to the stand.

Prior to the period when the female boreal owl permanently occupies the nest cavity (see below), pair behavior in the nest stand appears to be directed toward courtship feeding, checking potential nest cavities, and reinforcing the pair's tie to the nest cavity. Copulation does not seem common prior to nest occupancy. During 8 nights at nests of 3 radio-marked pairs during the final 2 weeks of courtship only once did the birds appear to copulate. Courtship feeding, however, appeared to be routine, taking place at or near the future nest cavity. For example on 29 April 1985, the following sequence was observed. At 2010 hr, the female flew to and entered the cavity while the male entered the nest stand at 2020 hr. At 2030 hr, the male flew to a tree 7 m from the cavity and sang. After the observer moved and scared the owl from the perch, the male flew to the cavity at 2110 hr, calling as he flew, while the female chirped from the cavity. The male flew to the cavity entrance for an instant before flying upstream barking twice. By 2145 hr, he returned to the cavity which the female had vacated. He entered the cavity, gave 2 series of staccato call and flew from the nest stand. A second example illustrating the brief encounters experienced during courtship feeding occurred on 7 April 1987. At 2034 hr, a radio-marked male began singing 30 m from the nest tree until the female cheeped from the vicinity of the nest at 2036 hr. At 2041 hr the male flew into the cavity and began singing loudly from the cavity entrance at 2044 hr for one minute changing to a soft continuous call when the female flew to a neighboring tree and began chirping. The male called softly until the female flew to the cavity at 2047 hr. He then gave one loud call and left the cavity immediately. The radio-marked female was still in the cavity when the observers left at 2130 hr.

On 2 nights we saw a mated female inspecting cavities within the courtship 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 from 3 female owls. These birds began roosting in the nest cavity 10, 19, and 22 days prior to egg laying. 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. B0107 in 1987 occupied the cavity every other day for the first week of nest occupancy before spending consecutive days on the nest. On the other hand, B058 in 1984 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 occupying cavities during nesting, we never found a boreal owl roosting in a cavity in 882 roost locations.

Females consistently first occupied the nest cavity in mid-to-late April. Six recorded occupancy dates over 4 years ranged from 13-23 April. In 1987, one bird laid eggs by 12 April indicating an earlier occupancy date. Laying dates appear more variable than occupancy dates, ranging 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. A majority of our data on laying dates came from radio marked birds so we know these observations do no represent renesting dates.

Females occupy the nest cavity day and night through incubation and most of the nestling period. We will discuss daily activity of male and female boreal owls during nesting more carefully elsewhere (Hayward et al., in prep). 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 14).

PREY POPULATIONS

Our observations show that boreal owls at Chamberlain captured a broad array of small mammals, a range of small birds, and a limited number of insect species. The availability of these prey differed throughout the year and across habitats.

Seasonal Prey Availability

Throughout the annual cycle, the availability of birds, insects, and small mammals changed dramatically. Although we did not measure bird abundance, we did record the presence - absence of forest bird species during winter, spring, and summer. During winter, from January through mid March, we recorded 10 species of passerines or woodpeckers during each of 4 years. The range of potential avian prey increased rapidly between mid March to May as migrants and species which winter at lower elevations moved into the study area. A minimum of 29 species of forest passerines or woodpeckers were recorded in the basin during spring or summer each of 4 years. The predominant insect prey recorded at Chamberlain, crickets of the family Gryllidae, generally overwinter as eggs. During periods of snow pack and early spring these prey would be unavailable to boreal owls.

Like other prey, availability of most small mammals decreased during winter as a result of snow pack and hibernation by some species. Pocket gophers and chipmunks were never captured during mid winter. Jumping mice appeared to hibernate well into spring as our sample of prey didn't include these mice until mid May. The arboreal flying squirrel is the only common mammalian prey whose availability likely did not decrease during winter.

Snow cover influences availability of mammalian prey for several months each winter. We measured snow depth in a level lodgepole pine forest from January through April at 5600 feet each winter from 1985-1987. This elevation represents the lowest extent of home range of all owls observed during the study. Snow depths exceeded 50 cm. until 16 March and 4 March in 1985 and 1986 respectively, but never reached 50 cm. in 1987. Snow depths exceeded 25 cm. until 7 April, 26 March and 30 March in 1985, 1986, and 1987 respectively. Above 6000 feet elevation, where owls spent a majority of their time in winter, snow depths exceeded 1 m for several months in most winters. On 4 April 1987, a year of below normal snow pack, our field notes indicated no bare ground above 6500 ft., and very few tree wells. Snow depths at this elevation exceeded 1 m in many areas on that date. These observations demonstrate that boreal owls must capture small mammals from forest covered with a nearly complete snow pack of 0.5 m or more during several months each year.

Small Mammal Habitat Use - Comparison of Sampling Methods

Because small mammals account for 81% of the boreal owl diet at Chamberlain, we used snap and pit trapping to study habitat use by small mammals. 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.

The most striking difference in pit trap and snap trap samples was the abundance of pocket gophers in the pit trap sample (Tables 16, 17). Pit traps captured pocket gophers on 5 sites while snap traps did not capture gophers. As expected pit traps also captured salamanders and frogs which snap trap did not sample.

Redback voles, shrews, and deer mice were the most frequently captured species by both methods. To compare the 2 trapping methods we looked at the capture rates for these 3 small mammals across 6 vegetation types using the 2 trapping methods. Capture rates of redback voles in pit and snap traps were strongly related(Spearman rank correlation, Rs = 0.94). The 2 trapping methods also resulted in similar ranking for shrew abundance (Rs = 0.75). Capture rate for deer mice differed (Rs < 0.10) mainly because pit traps in Douglas-fir forests capture few mice while the snap traps index was highest for this habitat. Otherwise the rank order of the habitats were similar for snap and pit traps.

Vegetation Association of Small Mammals

Below we will treat each species of small mammal separately and describe differences in capture rates in 7 broad vegetation types; 2 non forested types - mesic meadow and sage-bunchgrass, and 5 forested types - lodgepole pine, mixed conifer, Douglas-fir, wet spruce fir bottom, and spruce-fir upland. All forested sites were mature or older forest.

Redback voles were captured in both pit and snap traps substantially more frequently in spruce-fir forest than other types. 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 over an order of magnitude. Redback voles occurred in all forest types but capture rates were very low in lodgepole pine and dry mixed conifer forest. In both spruce-fir and Douglas-fir forests the biomass of red backed vole captures exceeded that of any other small mammal. We did not capture redback voles on non-forested sites.

We combined Sorex vagrans and Sorex cinerius for discussion of distribution and abundance because the species appeared to be found together in most habitats but required microscopic examination of skulls to identify accurately. Shrews occurred in all habitats. We captured shrews at all pit trap sites and variation in capture rates among habitats was lower for shrews than any other small mammal. Shrews were captured by both trapping methods most frequently in spruce-fir forests, including both spruce bottoms and upland spruce-fir forests. More shrews were captured in pit traps than any other species in lodgepole pine, mixed conifer and unforested habitats.

We captured deer mice in all vegetation types except wet meadow. The result of pit and snap trapping, however, lead to different ordering of habitats. Deer mice (caught in pit traps) were the most frequently captured small mammals on sagebrush slopes - the habitat where deer mouse pit trap captures were most frequent. Deer mice were often captured 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. During 2 years of snap trapping in the spruce-fir grid no deer mice were caught.

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

Mountain voles (Microtus montanus) and long-tailed voles (Microtus 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 non-forested habitats. Microtus capture rates were higher at sage sites than in wet meadow.

Pocket gophers, jumping mice, and heather voles were all caught in several habitats types, 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 and lodgepole habitats. Jumping mice were found in a variety of forest and non-forest habitats, but were never captured at our Douglas-fir or spruce-fir sites. 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 non-forested types.

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

Microhabitat Relationships of Small Mammals

In the preceding section we described broad habitat associations of small mammals. Below we will examine further the relationships between forest structure and small mammal capture rates using principal component analysis.

Six gradients of forest structure available at Chamberlain were identified from analysis of 101 stratified random plots measured in 4 broad cover types. We described the patterns of forest structure under Available Forest Structure and reported the characteristics of 6 principal components. Using the first 6 principal components from the above analysis we compared forest structures measured at 14 forest pit trap sites to the number of mammals captured at each site.

Spearman rank correlation between principal component scores and capture rate for 4 small mammal species suggested differences in habitat used (we considered $\underline{P} < 0.10$ as sufficient evidence to suggest a relationship and $\underline{P} < 0.05$ as strong evidence). In this analysis we considered only those small mammal species captured in at least half the 14 forested sites during 4 years of trapping. Redback vole capture rates were positively related to complexity of forest structure - PC1 (Spearman Rank Correlation (Rs) = 0.61 $\underline{P} = 0.02$) (Table 15). Shrews appeared to respond positively to increased forest complexity (PC1), increasing number of canopy layers, forest age and to sites without heavy grass or beargrass cover (PC5). The presence of a complete upper forest canopy or high density of 15-23 cm dbh trees appeared to be associated with reduced shrew capture rate (PC4). Deer mouse capture rate was not significantly correlated with any of the principal components suggesting that the mice respond to factors unrelated to the forest structure characteristics we measured or are simply ubiquitous in these forest habitats. The response of chipmunks to habitat structure contrasted with the other small mammals examined. The sign of correlations between chipmunks and principal components were opposite those of redback voles and shrews. Chipmunk captures were especially less abundant in forest with complex structure, high vertical diversity, and many large trees or forests with dense cover 0-2m above the ground (PC1 and PC2).

Small Mammal Biomass and Habitat Structure

In the previous 2 sections we looked for associations between trapping indexes for individual small mammal species and habitat characteristics. We can expand our picture of the distribution of boreal owl prey by ranking habitats by the abundance or biomass of small mammals. We used our pit trapping data to rank the habitats because this technique sampled a broader range of the available nocturnal mammalian prey and our sample included several sites in each vegetation type. We ranked habitats by average biomass of nocturnal mammals captured per 10,000 trap nights from 1985-1987 (this excluded ground squirrels, chipmunks, weasels, and flying squirrels captured in pit traps). Habitats ordered from high to low biomass were: spruce-fir upland (1559 g/10,000 trap nights), lodgepole pine (1168 g), sagebrush (1165 g), spruce-fir bottom (1141 g), Douglas-fir (1019 g), wet meadow (578 g), and mixed-conifer (433 g) (Fig. 5). Although trapping rates in spruce-fir upland stand out above the others, the biomass of small mammals captured in lodgepole, Douglas-fir, spruce-fir bottom, and sage habitats differ little. Mixed conifer and wet meadow had decidedly lower capture rates.

The ranking of these habitats assumes that each mammal species was captured in proportion to its abundance at the site and that our trap sites reflected the abundance of mammals in the designated vegetation types. Because some species of small mammals at Chamberlain appear to fluctuate in abundance and species are not distributed evenly across habitats our results refer only to the years we trapped. The rank order of habitats would change as the abundance of important mammal species fluctuate.

Year to Year Variation in Small Mammal Capture

We explored year to year variation in spring small mammal abundance in forested habitats using our snap trapping results. Although we trapped more sites with pit traps, than snap traps, we could not use pit trap data because we checked pit traps in different months, in different years. Therefore defining each year in pit trap samples was difficult.

We wished to compare estimates of available prey biomass within the study area between years. Therefore we multiplied the small mammal biomass captured on each site by the estimated percent cover of that habitat within the study area, prior to summing the biomass captured at all sites in a given year. The capture data did not include pocket gophers, flying squirrels, or chipmunks.

Our snap trap sample did not include results from some sites in particular years. These missing data were estimated using the average capture rate for that site from all other years. Of 25 cells in the 4 year by 5 site matrix, values for 4 cells were estimated. This manipulation likely masked differences among years but we can not be certain of the impact.

Because some data were estimated, conclusions from this analysis are supported by relatively weak evidence. Furthermore, this index does not reflect the influence of variation in abundance of important prey species like Clethrionomys relative to less important prey or the foraging habitat preference of the owls.

The trend in small mammal captures showed a decline from 1984 - 1986 with a slight recovery in 1987. Index values for each year 1984-1987 were 152, 133, 95, and 113. The capture rate in 1984 was 1.6 times larger than the 1986 value. Unfortunately, we can not test the significance of differences among years in capture rate.

DISCUSSION

As recent as ten years ago we did not recognize boreal owls as breeding residents of the northern Rocky Mountains. Based on the observations reported above, how should we now view this species - what is the current picture of boreal owl ecology? Are boreal owls becoming more abundant, less common, or maintaining stable populations in the Rocky Mountains? How does the species' geographic distribution, patterns of habitat use, and population biology fit in a strategy of regional forest management? These same questions arise whenever we first learn the basic natural history of a species. Most frequently the questions can not be directly answered but evidence from field observations can be used to build a case to support one view or another. Below we discuss how our observations lead toward answers to the important broad questions.

REGIONAL BREEDING DISTRIBUTION

Limited surveys for boreal owls in Idaho, Montana, Wyoming, and Utah revealed that boreal owls inhabit high mountain habitats over a broad region in the northern Rocky Mountains. During these surveys, boreal owls were located on most forests where biologists surveyed for more than 5 nights in high elevation forest during March or April. Based on the success of these surveys we expect that boreal owls inhabit much of the high elevation conifer forest in the region.

Our sample of owl breeding sites throughout the Northern Rockies suggests that boreal owl nesting occurs primarily in high elevation coniferous forest, especially spruce-fir. These forests cover only a small portion of the landscape and occur as islands in the expanse of forested land. Therefore, populations of boreal owls naturally exist as geographic isolates connected through movements of adult owls and dispersal of juveniles.

Information from U.S. Forest Service (USFS) timber data base suggests the extent of potential boreal owl habitat in the Northern Rockies. (We obtained estimates of the aerial extent of various forest types through USFS regional data bases.) Within USFS Region I, 9.2% of the forest land supports spruce-fir forest 15 cm dbh or larger (James W. Laux, Timber Management Planner, Region 1, USFS, pers. commun.). On seven Forests in Idaho south of the Salmon River, spruce-fir forest covers 6.7% of the forested landscape (Henry A. Cheatham, Timber Management, Region 4, USFS, pers. commun.). The spruce-fir forest within the region occurs in patches of varying extent separated from neighboring patches by landscapes supporting an extreme range of vegetations. The value of individual islands of spruce-fir forest to boreal owls will likely depend on the island size, distance to nearest neighbor, vegetation surrounding the island, and the quality of habitat within the island (MacArthur and Wilson 1963, Diamond 1975, and others).

How these landscape pattens 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. Loss of spruce-fir forest will reduce patch size and increase the distance between suitable forest habitat. Both processes have been linked to increased rates of local extinction (MacArthur and Wilson 1963, Connor and McCoy 1979). Reductions in the size of forest habitat will reduce the numbers of owls in breeding populations. Because boreal owl populations inherently exist at low density, reduction in population size could lead to demographic instability and extinction due to stochastic events. Reductions in patch size could also lower the rate of immigration from neighboring populations. Extensive forest fires throughout the region in 1988 demonstrated how quickly the area of suitable habitat can be reduced.

FORAGING HABITAT

We were unable to directly observe foraging habitat use and therefore must rely on indirect evidence to evaluate whether boreal owls seek certain forest types to hunt. Both roost habitat use and food habits hint at owl foraging habitat.

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 occupied spruce-fir forest 35% and lodgepole 38% of the time. The frequent use of spruce-fir forest contrasts with the availability of spruce-fir in the area. Spruce-fir covers less than 10% of the study area while lodgepole covers over 50%.

Food habits information and data on habitat use by small mammals supports the contention that spruce-fir forest is important foraging habitat year round, but especially in summer. During both winter and summer redback voles were by far the most frequently captured prey (Table 10), especially in years when the owls bred most successfully.

Our small mammal studies showed that redback voles were not equally abundant at all trapping sites and suggested that over-all, small mammal biomass differed between types. Spruce-fir forest supported the greatest number of redback voles and highest small mammal biomass. Redback voles were far more abundant in spruce-fir forests than any other habitat we trapped. We captured nine times as many redback voles in an old spruce-fir forest than we captured in any other forest type. The voles appeared absent from open habitats. Lodgepole pine supported fewer voles than other forested habitats while Douglas-fir forest and mixed conifer support fewer voles than the spruce-fir sites. Total biomass of small mammals appeared to be lowest in lodgepole pine habitats. Biomass on sage slopes, and forest sites other than lodgepole, did not differ as substantially.

These observations of owl food habits and habitat use by small mammals would suggest that boreal owls hunted often in spruce-fir forests where redback voles are most abundant. Of course, predicting foraging habitat from food habits information is risky. Roost habitat use discussed above, however, supports the conclusions reached from food habits data.

The high use of spruce-fir forest in summer fits especially well with the food habits and prey habitat data. The evidence points to old spruce-fir forest as the most important summer foraging habitat. During winter the owls spent considerable time in spruce-fir forest where redback voles are most abundant but used lodgepole pine habitats most. The high consumption of redback voles but frequent use of lodgepole habitats during winter are not easily explained. The influence of snow cover on prey availability in different forest types is not understood, but the more shallow snow cover typical in lodgepole at Chamberlain may alter prey availability relative to other habitats. Also, the behavior of small mammals in various forest types may differ. Whether prey is more available in lodgepole pine forest is not known.

Interestingly, a majority of flying squirrels captured by female boreal owls in winter were in lodgepole habitats. The long, clear bole of lodgepole trees in these stands likely give the owls access to squirrels which are more effectively protected by foliage in other forest types.

HABITAT USE FOR NESTING, ROOSTING, AND FORAGING

Boreal owls at Chamberlain used particular forest habitats for nesting, roosting, and foraging. Our observations provide evidence that both nesting sites and roost sites are not randomly drawn from available habitats. When we compared stand structure at nest sites and random sites the distribution of nest sites fell within a narrow range of available structures. Likewise, forest structure at roost sites differed from random locations, especially in summer. These results suggest the owls choose particular habitat features for nesting and roosting. Our observations did not permit a similar analysis of foraging habitat use. As suggested in the previous section, however, several types of evidence suggest that mature spruce-fir forest is hunted extensively even though this is not the most abundant forest type.

The resources required by owls for nesting, roosting, and foraging were not all provided by any single forest type. Nesting habitat must provide suitable nest cavities and a high probability of encountering a mate; roosting habitat must moderate extreme weather conditions and provide concealment from predators; while foraging habitat must facilitate location and capture of prey. These needs are met by forests which differ in structure.

Nesting Habitat.--The owls appear to search for nest cavities in habitats where cavities are most abundant. Because boreal owls use large tree cavities, only mature and older forest with large trees and snags contain numerous potential nest sites. We believe the consistent forest structures found at boreal owl breeding sites do not result from preference for mature forest structure *per se*. Rather, the owls key on forests with this structure because the probability of encountering suitable nest cavities is highest in these forests. The density of suitable cavities is extremely low in other forest types at Chamberlain. Although we did not measure cavity density we feel density of large cavities may be nearly 2 orders of magnitude greater in mixed conifer and aspen forests (the forest types used for nesting) than in lodgepole or spruce-fir forest.

Several observations indicate that nesting owls require more than a site with a cavity. During our nest box experiment, owls did not nest in lodgepole pine despite the provision of suitable cavities. Further-more, at Cold Meadows we never observed boreal owls nesting in lodgepole types although in this study area, lodgepole pine supported some large cavities.

Regional observations indicate that nesting habitat may vary geographically. Our observations of nesting habitat at Chamberlain contrast with sites found elsewhere in the northern Rockies. While few owls nested or sang in spruce-fir forest at Chamberlain, over three quarters of the regional sites occupied spruce-fir forest. Fire history and geography at Chamberlain may have created a relatively unique situation with low nest site availability in spruce-fir but abundant cavities in adjacent Douglas fir forest. As a result of fire, few old spruce-fir stands which support large snags remain in the basin. Instead, the influence of fire and climate have led to high elevation, old, mixed Ponderosa - Douglas-fir within the normal spruce-fir zone. Cavities from pileated woodpeckers in the Ponderosa pine snags provide abundant, high quality owl nest sites. Few forests outside the wilderness had the unique juxtaposition of habitats found at Chamberlain. Throughout most of the region, Douglas-fir habitat types supporting large Ponderosa pine are not perched within the spruce-fir zone. In forests without Ponderosa pine boreal owls are forced to find cavities in subalpine-fir, spruce, lodgepole, or Douglas-fir trees which don't form the quality, persistent cavities found in Ponderosa pine.

Despite the variation observed in nesting habitat, forest with a complex structure was commonly used. Sexual selection could explain some of the consistency in structure of nesting habitat. During years when boreal owl populations are low, owls may have difficulty locating potential mates. Colwell (1986) has argued that breeding habitat selection may be driven by sexual selection for species with low population densities. Individuals who choose a distinct breeding habitat, recognized as breeding habitat by other members of the population, may increase the probability of encountering a mate. Because boreal owl densities appear to be quite low, locating potential mates may be a challenge in some years. Similarly, competition with other owls may restrict the distribution of boreal owls (Hayward and Garton 1988). Saw-whet (Aegolius acadicus), western screech (Otus kennicottii), and great-horned owls (Bubo virginianus) are all more abundant at lower elevations in the RNRW.

We cannot test various explanations but suggest that alternate hypothesis of cavity availability, sexual selection, physiological tolerance, predation, and competition may be reasonable explanations for the restricted elevation distribution of boreal owl nesting habitat. These hypothesis are not mutually exclusive.

Roost Habitat.--Roost sites differed considerably from breeding habitat and from random locations at Chamberlain. At roosts, density of small trees was high, canopy cover was high, and basal area was low compared to nest sites. Forests with open structure used for nesting were not used for roosting. Our observations showed that winter roosts differed only slightly from random sites while summer roosts appeared unique. Site choice appears most critical in summer. Temperature measurements and observations of owls gullar fluttering indicate that moderation of high summer temperatures is an important function of summer roosts. Roosts also must provide protection from rain and concealment from predators, particularly avian predators.

Our observations of owl roost perch positions within the tree suggest that owls do not choose roost perches randomly. Aspect of roosts and position in the tree appeared to be important to the owls. Our measurements of weather conditions at roosts and cover around roosts, however, did not provide insights into why owls choose particular roost perches.

Owls change perches apparently in response to the weather. On hot days in summer owls frequently moved soon after direct sun shone on the perch. During winter the owls frequently moved in response to high wind and witches brooms provided overhead protection during heavy rain. Conversely, we were frequently surprised by the tolerance boreal owls had for wind, snow, and cold. Although owls always sought shelter from rain, the birds often perched unsheltered from snowfall. Normal winter temperatures at Chamberlain may not stress boreal owls which are well adapted for cold. The thermal neutral zone of the owl may encompass a majority of the temperatures experienced during winter in this region.

Warm summer conditions appear to stress boreal owls at Chamberlain more severely than winter weather. Behaviors to ameliorate warm conditions may involve roost stand selection to a larger extent than perch choice.

Although it appears that perch choice is influenced by thermoregulation, we suggest that avoiding predation and mobbing by jays and passerines may also be important. The fact that 74% of all roosts were next to the tree bole cannot be easily explained by examining wind direction, wind speed, and temperature. By roosting next to the bole of a 25 cm diam tree, the owl is completely obscured from the view of predators for an arc of about 55^0 and no more than half its body is visible for over 90^0. Unlike a roost in dense foliage, a perch next to a tree facilitates quick escape in a number of directions and allows the owl to view the ground for prey and its surroundings for enemies. Finally the bole of the tree prevents the silhouette of the owl from being observed from many directions further inhibiting detection by predators.

Foraging Habitat.--The resources provided by foraging habitat differ from those of nesting and roosting habitat. Our analysis of foraging habitat, however, links roosting and foraging sites. We feel that, because boreal owls hunt over large areas each night, usually several km from the nest, they can not afford to return to particular roost sites. Instead they choose a suitable roost from the forest near the end of the foraging bout. Therefore, forest types necessary for foraging and roosting do not appear to differ. We suspect that optimum foraging habitat - sites providing suitable flight paths for foraging and attack as well as abundant prey - is more limited than roosting habitat.

LARGE HOME RANGE REQUIREMENTS

Boreal owls at Chamberlain used large home ranges. The average size of winter and summer ranges compare with those cited by Lindstedt et at. (1986) for coyote (Canis latrans), fox (Vulpes vulpes), fisher (Martes pennati), and pine marten (Martes americana). Among owls, our estimates of boreal owl ranges compare, and in some cases exceed, those reported for larger species. Forsman et al. (1984) reported home ranges less than 2000 ha for spotted owls (Strix occidntalis), Hirons (1985a) reported Tawny owl (Strix aluco) territories less than 100 ha in England, Bull (1989) measured great-grey owl home ranges which averaged 6730 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 of Europe (Mikkola 1983).

Several factors likely contribute to large boreal owl ranges. As discussed above, no single forest type provides optimum nesting, roosting, and foraging habitat. At Chamberlain, mixed conifer stands have numerous large snags used by Pileated woodpeckers for nesting. These stands lie on the eastern side of the study area at lower elevations as do aspen stands which contain many potential nest cavities. Spruce-fir forests used for roosting and foraging, especially during summer, are concentrated at high elevations to the west. Therefore, geographic features lead to a broad dispersion of resources forcing the owls to move long distances.

Low productivity of small mammals throughout Chamberlain also contributes to large owl ranges. Lindstedt et al. (1986) showed that home range size among carnivores is related to prey production. Results of small mammal trapping at Chamberlain suggest that abundance of mice and voles is quite low (Table 15) 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 per 100 trap nights during a week of trapping each spring for 2 years. We also caught 5.6 shrews per 100 trap nights, or 13.9 small mammals per 100 trap nights. On the next most productive forest site, an old Douglas-fir forest, we caught 0.9 mammals per 100 trap nights; this sample did not include any shrews. Our trapping rate at the spruce-fir site was similar to snap trap capture rates reported by Lofgren et al. (1986) and Korpimaki (1987a, 1987b) during 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, 1987b) captured up to 18 voles per 100 trap nights in Finland during peak vole years. Our trapping rates in habitats other than spruce-fir, however, 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 which may support the greatest abundance of mammals constitute only a portion of the spruce-fir forest. Therefore we suspect 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. Some boreal owls at Chamberlain exhibited extremely long courtship which may indicate poor prey conditions. 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 considerable nourishment from her mate to build up 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 feeding 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 one spruce-fir stand to the next.

ROLE OF BOREAL OWLS IN THE COMMUNITY

During our studies at Chamberlain, boreal owls appeared to be the most abundant avian predator of forest small mammals. Pygmy (Glaucidium gnoma), saw-whet, great-horned, great-grey (Strix nebulosa), barred (S. varia), western screech, and long-eared (Asio otus) owls were heard infrequently even in good calling years. Pygmy and boreal owls were the only owls found dispersed throughout the basin. Pygmy owls consume a wide range of prey; small mammals account for under 50% of their diet (Earhart and Johnson 1970). Diurnal raptors were also uncommon and none of the species found in the region concentrate on forest small mammals.

Other important small mammal consumers at Chamberlain included pine marten, weasels (Mustela spp.), fisher (Martes pennanti), and coyote. The relative influence of these predators on small mammal distribution and abundance compared to boreal owls can not be addressed with our data. Some differences are obvious, however. During winter boreal owls can attack only prey which reach the snow surface or a few cm beneath. We observed sign of both weasel and pine marten tunneling at the ground surface under 1 m or more of snow. During summer, dense shrubs and grass hinder the owl more than mammalian carnivores. Availability of small mammals, then, differs between boreal owls and other taxa.

The small mammals which boreal owls prey upon indirectly influence forest regeneration and growth. Pocket gophers can significantly reduce seedling survival through clipping and root damage (Dingle 1956, Hooven 1971). Deer mice consume conifer seeds and may significantly influence the distribution and density of conifer seedlings (Williams 1959, Halvorson 1982). Redback voles and flying squirrels feed on fungus and may play important roles in dispersal of micorhizal fungi (Maser et al. 1978, Fogel and Trappe 1978, Martel 1981). Through herbivory and seed predation these small mammals also influence the distribution and production of shrubs, grasses, and forbs in the forest.

Reactions of the small mammals to boreal owl predation could influence the plant herbivore relationships between the small mammal community and forest vegetation. Boreal owl predation on shrew populations, which themselves prey upon mice and voles, may exert an indirect effect on forest vegetation. Whether boreal owl predation influences small mammal abundance and distribution in the northern Rockies in unknown. The consequences of boreal owl predation, however, may be important for forest management in the spruce-fir zone. A crude estimate of small mammal consumption by boreal owls (based on our observations of nesting owls) indicates that an adult pair which raises 2 nestlings to four months old would kill about 2000 voles, pocket gophers, shrews, and mice in a year.

Boreal owls may also influence the distribution of other owls inhabiting the basin (Hayward and Garton 1988). Saw-whet owls which are congeneric with boreal owls, are the most abundant Strigiform at lower elevations in the River of No Return Wilderness (Hayward and Garton 1988) but were rarely heard at Chamberlain during this study. Whether physiological limitations or competition with boreal owls restrict saw-whet owls is not clear. The similarity in food habits and habitat use by these species and the fact that saw-whets occur in colder portions of the wilderness suggest that competition may play a role.

VARIATION IN BREEDING DENSITY

Throughout the ecological literature wide fluctuations in vertebrate populations have been associated with high latitudes (Finerty 1980). Korpimaki (1986) reviewed patterns in population fluctuations of Aegolius funereus in Europe. He noted a positive relationship between the magnitude of fluctuations and latitude but also a relationship with snow depth. Microtine fluctuations increased northward as did synchrony, while alternate prey increased southward. Site tenacity by the owls decreased northwards. These factors promote instability in northern European, and stability in central European, boreal owl populations.

Boreal owls at Chamberlain exhibited instability in breeding effort and breeding success during our four year investigation. Several indexes of adult breeding population abundance dropped during the second and third years of study but recovered during the fourth year. Nest failure due to factors other than predation also were greater during the second and third year. Unfortunately we did not have a reliable estimate of adult population density or a method to monitor productivity of numerous nests. Therefore it is difficult to determine the magnitude of population fluctuations occurring during this study and compare them to information from Europe. The virtual silence we observed from all species of owl in 1986, however, suggested a large change in breeding activity compared to 1984, 1987, and 1988. Variation in both fledging success and numbers of breeding owls, then, appears to be high at Chamberlain.

POPULATION VIABILITY

Is the population of boreal owls at Chamberlain self sustaining? As we will suggest below, current evidence indicates the population of boreal owls at Chamberlain could experience periodic local extinction. Other populations in the northern Rockies may experience similar negative growth and rely on immigration to sustain viability. Natural, nomadic movements of individuals inhabiting many dispersed breeding populations and periodic bursts of reproduction likely maintain the species on a regional scale. Because boreal owls exist in an island environment with unstable prey production and wide variation in breeding populations, however, the long term stability of the species under conditions of intensive forest management may be questionable.

Our observations at Chamberlain suggests a population whose status is marginal. Individuals maintain very large home ranges, nestling production is low, and few individuals attempt to breed in some years.

The evidence for low reproduction and high mortality at Chamberlain contrasts with population data from European populations. We observed the fate of 16 nests at Chamberlain and measured the clutch size of 2 others. Nest failure was an important component of low production; 62.5 % of the nests failed. Clutch size and fledging were also low. Completed clutches averaged 3.1 eggs (N=11) and fledging rate for nests which fledged young averaged 2.33 young (N=6). In Europe, boreal owls produce far more young. In Finland, during a 13 year study, Korpimaki (1987b) 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 failure averaged 23%. Solheim (1983) reported an average fledging rate of 4.8 young from first nests of polygamous boreal owls in Europe. Biandrious females produced up to 12 young in a year. In Germany, Konig (1969) reported fledging rates of 4 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 at Chamberlain.

Adult survival in Europe may also exceed average adult survival at Chamberlain although estimates for both regions are based on limited data. Our most optimistic assumptions lead to an annual survival estimate of 46%. Franz et al. (1984) as cited by Korpimaki (1988) reported female adult survival as 78%.

Only under our most optimistic estimates of survival and fecundity in a simple population growth model (Leslie matrix projection) was the boreal population at Chamberlain stable from 1984-1987. This simulation (No. 1) assumed all nest failures during the study were human caused and therefore not representative of the population (we actually feel only one of 10 failures was human caused). All nests, then, were assumed to fledge 2.33 young per year and no nests failed. All females were assumed to breed each year, to raise one brood per year, and to fledge 50% female offspring. Owls were assumed to breed in the spring following birth and all age classes reproduce at the same rate. Adult survival was estimated at 46% assuming all emigration observed during the study was complemented by equal immigration and all dispersing owls survived. Finally, juvenile survival was assumed equal to our estimated adult survival.

We ran a Leslie projection (Leslie 1945) to look at population growth using 9 age classes with complete mortality at age 9 (Korpimaki 1988). Using this model structure, age class 7 includes less than 1% of the population. This model lead to a stable population; $\lambda = 0.99$ (Simulation No. 1).

A more realistic, but still optimistic model (simulation No. 2) assuming some nest failure and higher juvenile mortality indicated rapid population decline; G = 0.65. Juvenile survival was set at half the adult rate and nest failure at 23% as measured by Korpimaki (1988). For this simulation all assumptions of a Leslie projection remain and other population parameters were set as in the first simulation.

Both the above results were disturbing because only very optimistic input parameters lead to a stable population. The projected population decline is especially alarming in the more realistic case (simulation No. 2). Even in the second simulation, however, fecundity was higher than we measured in this study. The fecundity rates estimated for Chamberlain (see Owl Population Characteristics) do not include radio-marked females who did not attempt to mate. Therefore these are optimistic estimates. Our survival estimates, on the other hand, have broad confidence intervals and therefore we can not place too much emphasis on the mean value. We therefore ran 2 more simulations using the 95% bounds on survival under the assumption that owls who emigrate, live. For these simulations fecundity was set at the average for all nests monitored at Chamberlain. Simulation no. 3, using the upper bound on survival (91%) and assuming juvenile survival is half the adult rate suggests slightly positive growth ($\lambda = 1.02$). When survival is set at 23%, the lower bound, and juvenile survival at half the adult rate, population decline is precipitous ($\lambda = 0.28$).

From these simulations we must conclude that the population of boreal owls at Chamberlain likely is not self sustaining. Although our evidence is weak, no other information on boreal owl population growth in North

America exists. We hypothesize that during good breeding years the population experiences modest positive growth but during poor years population decline is extreme. During our studies good and poor years appear equally common. Under this hypothesis, the boreal owl population at Chamberlain relies on immigration to sustain itself.

On a broader scale, boreal owl populations may experience positive growth during most years in regions which are more productive than Chamberlain. 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 Chamberlain, then, may in some situations depend on managed forest for long term viability. The impact of silvicultural practices in productive spruce-fir forest may influence not only the local boreal owl population but also distant populations.

MOVEMENTS AND POPULATION VIABILITY

Year to year movement patterns of boreal owls observed at Chamberlain and in Europe support the scenario outlined above. Wallin and Anderson (1981), Solheim (1983), Lofgren et al (1986), and Korpimaki (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 while females were tenacious only during prey peaks. At Chamberlain, boreal owls showed a mixed strategy of site tenacity and nomadism. Clearly the owl's life history would facilitate recolonization of locally extinct habitats through immigration. Production in some populations, however, must be sufficient to produce high net emigration rates.

CONCLUSIONS

Prior to this investigation very little was known of the biology of boreal owls in North America. Therefore even relatively trivial observations often added to our understanding of the species. Several results however appear most striking. Those include:

1) Boreal owls in the northern Rocky Mountains occur in a relatively narrow life-zone, breeding predominantly in forests of the spruce-fir zone. The species' limited elevation distribution and regional geography together result in a natural distribution pattern with numerous breeding populations isolated on islands of high elevation forest separated by regions of lower elevation.

2) Although we could not directly record foraging habitat, several types of evidence suggest that mature and older spruce-fir forest is important for foraging. It is difficult, however, to separate selection for roosting and foraging habitat.

3) At Chamberlain, no single forest habitat provides optimum conditions for nesting, roosting, and foraging. The owls actively selected habitat using sites which differ in structure from random locations. Forests chosen for nesting and roosting provide very different resources, meeting special needs of the owls.

4) Owls at Chamberlain maintained large seasonal home ranges and moved long distances from day to day. The extensive movements result from several factors; the prevailing low productivity of the small mammal community, dispersed distribution of habitats with abundant small mammals, and the distribution of habitats suitable for nesting, roosting, and foraging.

5) Local geography at Chamberlain strongly influenced the daily and seasonal movements of boreal owls. The habitats with abundant cavities, providing optimum nesting habitat, were confined to low elevations on the eastern edge of the study area while spruce-fir forest, which supports the highest prey populations and cool summer roosts, was found at high elevations in the west. Therefore, resources used daily were not interspersed but segregated geographically.

6) In high elevation conifer forest, boreal owls represent the dominant avian predator of small mammals. As such, the species may have a significant indirect influence on ecosystem structure and function in localities where boreal owls are abundant.

7) Size of boreal owl breeding populations and breeding success fluctuated dramatically during the study. These fluctuations may be tied to availability of small mammals, especially redback voles.

8) Productivity of boreal owls at Chamberlain is low compared to populations in Europe, while adult mortality may be high. Considering the dramatic fluctuations in breeding production and the population data recorded at Chamberlain, we question whether this population is self sustaining. We hypothesize that the population may, at infrequent intervals, become locally extinct and rely on emigration to recolonize the basin or portions there-of. Likewise, this population may produce individuals in some years which emigrate and supplement other populations.

9) Because boreal owl populations are confined to the spruce-fir zone, the regional population occurs as an island population. The overall extent of spruce-fir forest in the region is limited. The island nature of the owls habitat coupled with the low rates of population growth recorded in this study suggest that forest management must accommodate the species needs if boreal owls are to remain an active part of the regional environment.

MANAGEMENT RECOMMENDATIONS

Our recommendations must be regarded as tentative. The results are based largely on observations of a single population of boreal owls in central Idaho. Until several other populations receive attention management must be approached cautiously.

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 will also support breeding boreal owl populations. Playback surveys conducted from January to April offer the most efficient means of determining whether potential habitat is currently occupied. A single year of negative results, however, does not constitute evidence that a site is not occupied. The yearly variation in calling rates we observed suggest that several years of surveys will be necessary to establish presence-absence.

Any attempt to monitor trends in abundance or productivity will require development of specific monitoring methods. Because we do not understand what factors, aside from breeding density, influence singing rates, playback surveys are not a suitable monitoring tool. A valid monitoring scheme will require a valid sampling design and new sampling methods.

HABITAT MANAGEMENT

Management of nesting habitat will largely involve snag management, management of large woodpeckers, and aspen management. Potential nest snags should be over 38 cm dbh and part of an intact forest stand. Our evidence indicates small stands, less than a hectare are suitable. Snags in mature or older conifer forest or aspen stands should be managed most vigorously. 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, however, we must look into how box dispersion, density, and other factors influence boreal owls and other members of the forest community.

Management of aspen forest will be an effective, straight forward method of providing nesting habitat. Large aspen trees were frequently used for nesting at Chamberlain although aspen forest was uncommon in the basin and individual stands usually covered less than 0.5 ha. Through management schemes which maintain a broad dispersion of aspen groves and which favor large diameter trees, managers can provide nesting habitat without conflicting with other resource values.

Roosting habitat can be maintained through proper management of foraging habitat. In this region, requirements of winter roosting habitat appear 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 appear to be strongly food limited and reductions in prey availability could be disastrous for populations which may not currently be self-sustaining. Silvicultural prescriptions must be written to maintain stands with abundant small mammals and stand structure which permits owl foraging flights. At Chamberlain mature and older spruce-fir forest with moderate canopy cover and patchy tree dispersion appeared optimal. We suggest that uneven age forest management could be adopted. A review of 14 National Forest Plans from Regions I and IV, however, demonstrate a reluctance to initiate uneven age management in many spruce-fir stands. Our interpretation of 14 plans indicated even age management would dominate on all but one forest.

Until we have evidence to the contrary, clearcuts and young forest stands can not be considered suitable foraging habitat. In Europe, boreal owls hunted clearcuts only during a short period after snow melt in spring (Sonerud et al. 1986) when vegetation was short and prey vulnerable. Because of their hunting behavior, boreal owls can only hunt the edge of clearcuts. Dense regeneration and pole stands can not be used efficiently because of restrictions on owl mobility.

DISTURBANCE

Evidence from Europe (Jacobsen and Sonerud 1987) and Colorado (Palmer, D. A. Colorado State Univ., pers. comm.) indicate boreal owls tolerate human disturbance. In Colorado, one nest site was adjacent to a major highway open year round. Boreal owls at Chamberlain tolerated repeated visits to weigh young at the nest.

We do feel the owls are susceptible to disturbance from the time the female first occupies the nest until after laying. One female disturbed during laying abandoned the nest for 2 days but returned to the nest and fledged 2 young. Another female disturbed prior to egg laying abandoned the nest and mated with a different male within 2 weeks.

LANDSCAPE

Because boreal owls use large home ranges and population densities are low, quality habitat must be distributed across a broad area. The area necessary to support a population is unknown but likely exceeds 1000 km^2. Throughout the landscape only a modest (unknown) percent of the area must remain high quality foraging habitat, but quality stands must be well dispersed.

Many individual populations must be maintained because of the high probability for local extinction of individual populations. Because spruce-fir forests are naturally limited due to geography and fire history, the manager will be challenged to maintain enough suitable habitat to support the species in the long term.

Management for boreal owls, then, is compatible with timber harvest and will not preclude use of forest resources. Rather, management which maintains boreal owl habitat will force us to approach forest management from a broad perspective and in a way which is more compatible with the dynamics of spruce-fir forest systems. Through uneven-age management, watershed, soil, recreation, and wildlife values will be maintained while wood fiber is extracted. Long term forest productivity will be enhanced because the system will not be stressed as it is through even-age cutting systems. Biological diversity will be maintained by retaining the, old forest structure and associated fungi, insects, plants, vertebrates, and ancient trees. Finally, even if only in a small way, uneven-age management for boreal owls will contribute less toward global warming by releasing lesser amounts of CO_2.

LITERATURE CITED

Alldredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 50:157-165.

Arno, S. F. 1979. Forest regions of Montana. USDA For. Sev. Res. Paper INT-218.

Avery, T. E. 1975. Natural resource measurements. McGraw Hill, NY.

Bondrup-Nielsen, S. 1978. Vocalizations, nesting, and habitat preferences of the boreal owl (Aegolius funereus) in North America. M.S. Thesis, Univ. of Toronto.

Bull, E. L., M. G. Henjum, and R. S. Rohweder. 1988. Home range and dispersal of great grey owls in northeastern Oregon. J. Raptor Res. 22:101-106.

Capen D. E. ed. 1981. The use of multivariate statistics in studies of wildlife habitat. USDA Forest Serv. Gen Tech. Rep. RM-87, Rocky Mountain For. and range Exp. Stat., Fort Collins, Colo.

Cline, S. P., A. B. Ber, H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir Forests, Western Oregon. J. Wildl. Manage. 44:773-786.

Colwell, R. K. 1986. Community biology and sexual selection: Lessons from hummingbird flower mites. Pages 406-424. in J. R. Diamond and T. J. Case. eds. Community ecology. Harper and Row, New York.

Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113:791-833.

Daubinmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci. 33:43-46.

Diamond, J. M. 1975. Assembly of species communities. Pages 342-444. in M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Mass.

Dingle, R. W. 1956. Pocket gophers as a cause of mortality in eastern Washington pine plantations. J. For. 54:832-835.

Dixon, K. R. and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Earhart, C. M. and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.

Finerty, J. P. 1980. The population ecology of cycles in small mammals: mathematical theory and biological fact. Yale Univ. Press.

Finklin, A. I. 1988. Climate of the Frank Church, River of No Return Wilderness, Central Idaho. Gen. Tech. Rep. INT-240. Ogden, UT.

Fogel, R. and J. M. Trappe. 1978. Fungus consumption (Mycophagy) by small animals. Northwest Sci. 52:1-31.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Mono. 48:1-64.

Franz, A., T. Mebs, and E. Seibt. 1984. Zur populations biologic des Raauhfusskauzes (Aegolius funereus) in sudliehen Westfalen und in angrenzenden Gebieten anhand von Beringungsergebnissen. Vogelwarte 32:260-269.

Fretwell, F. D. and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:16-36.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press. Cambridge, MA.

Hall, E. R. 1946. Mammals of Nevada. Univ. of California Press, Los Angeles.

Halvorson, C.H. 1982. Rodent occurrence, habitat disturbance, and seed fall in larch-fir forest. Ecology 63:423-433.

Hayward, G. D. 1987. Betalights: An aid in the nocturnal study of owl foraging habitat and behavior. J. Raptor Res. 21:98-102.

Hayward, G. D. and E. O. Garton. 1983. First nesting record for boreal owl in Idaho. Condor 85:501.

Hayward, G. D. and E. O. Garton. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. Oecologia 75:253-265.

Hayward, G. H., and P. H. Hayward and E. O. Garton. 1987a. Revised breeding distribution of the boreal owl in the Northern Rocky Mountains. Condor 89:431-432.

Hayward, G. D., P. H. Hayward, and E. O. Garton. 1987b. Movements and home range use by boreal owls in central Idaho. Pages 175-184. in R. W. Nero, C. R. Knapton, R. J. Hamre, eds. Biology and conservation of northern forest owls: symposium proceedings. U. S. For. Serv. Gen. Tech. Rep. RM-142.

Heisey, D. M. and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668-674.

Hirons, G. J. M. 1985a. The effects of territorial behavior on the stability and dispersion of Tawny Owl (Strix aluco) populations. J. Zool. Lond. (B) 1:21-48.

Hirons, G. J. M. 1985b. The importance of body reserves for successful reproduction in the tawny owl (Strix aluco). J. Zool., Lond. (B). 1:1-20.

Hooven, E. F. 1971. Pocket gopher damage on ponderosa pine plantations in southwestern Oregon. J. Wildl. Manage. 35:346-353.

Hurlbert, S. H. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Mono. 54:187-211.

Jacobsen, B. V. and G. A. Sonerud. 1987. Home range of Tengmalm's owl: A comparison between nocturnal hunting and diurnal roosting. Pages 189-192. in R. W. Nero, C. R. Knapton, R. J. Hamre, eds. Biology and conservation of northern forest owls: symposium proceedings. U. S. For. Serv. Gen. Tech. Rep. RM-142.

James, F. C. and C. E. McCullock 1985. Data analysis and the design of experiments in ornithology. pages 1-63 in: R. F. Johnson, ed. Current ornithology. Vol.2, Plenum Press, N. Y.

Jennrich, R. I. and F. B. Turner. 1969. Measurements of noncircular home range. Journal of Theoretical Biology 22:227-237.

Johnson, R.A. and D.W. Wichern. 1982. Applied multivariate statistical analysis. Prentice-Hall. Engelwood Cliffs, NJ.

Konig, C. 1969. Six year observations of a population of Tengmalm's owl Aegolius funereus. J. fur Ornithologic 110:133-147.

Korpimaki, E. 1986. Gradients in population fluctuations of Tengmalm's owl Aegolius funereus in Europe. Oecologia 69:195-201.

Korpimaki E. 1987a. Selection for nest hole shift and tactics of breeding dispersal in Tengmalm's owl Aegolius funereus. J. Anim. Ecol. 56:185-196.

Korpimaki E. 1987b. Clutch size, breeding success and brood size experiments in Tengmalm's owl Aegolius funereus: A test of hypothesis. Ornis Scandinavia 18:277-284.

Korpimaki, E. 1988. Effects of age on breeding performance of Tengmalm's Owl Aegolius funereus in western Finland. Ornis Scand. 19:21-26.

Laundre, J. W., T. D. Reynolds, S. T. Knick, and I. V. Ball. 1987. Accuracy of daily point-relocations in assessing real movement of radio-marked animals. J. Wildl. Manage. 51:937-940.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time and body size in mammals. Ecology 67:413-418.

Lofgren, O., B. Hornfeldt, and B. G. Carlsson. 1986. Site tenacity and nomadism in Tengmalm's owl (Aegolius funereus (L.)) in relation to cyclic food production. Oecologia 69:321-326.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

Martell, A. M. 1981. Food habits of Southern Red-backed Voles (Clethrionomys gapperi) in northern Ontario. Canadian Field Nat. 95:325-328.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

Mikkola, M. 1983. The owls of Europe. Buteo Books, Vermillion, South Dakota.

Orloci, L. 1979. Non-linear data structures and their descriptions. Pages 191-202. In: L. Orloci, C. R. Rao, and W. M. Stiteler. eds. Multivariate methods in ecological work. International Co-operative. Publ. House. Fairland, MD.

Palmer, D. A. 1986. Habitat selection, movements and activity of boreal and saw-whet owls. M.S. Thesis. Colorado State Univ.

Palmer, D. A., and R. A. Ryder. 1984. The first documented breeding of boreal owl in Colorado. Condor 86:251-217.

Pielou, E. C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley & Sons. N. Y.

Samuel, M. D., D. J. Pierce, E. O. Garton, L. J. Nelson, and K. R. Dixon. 1985. User's manual for program HOME RANGE. Univ. of Idaho, Forest, Wildlife, and Range Experiment Station Tech. Rep. 15.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoretical Population Biology 20:281-325.

Schoener, T. W. 1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

Scott, J. M., B. C. Csuti, J. D. Jacobi, and J. E. Evens. 1987. Species richness: a geographical approach to protecting future biological diversity. Bioscience 37:782-788.

Smith, D. G. and R. Gilbert. 1984. Eastern screech owl home ranges and use of suburban habits in southern Connecticut. J. Field Ornithology 55:322-329.

Solheim, R. 1983. Bigyny and biandry in the Tengmalm's owl Aegolius funereus. Ornis Scand. 14:51-57.

Sonerud, G. A., R. Solheim, and B.V. Jacobsen. 1986. Home-range use and habitat selection during hunting in a male Tengmalm's Owl Aegolius funereus. Fauna Norvegica, Ser. C. Cinclus 9:100-106.

Steele, R., R. D. Pfister, R. A. Ryker, J. A., Kittams. 1981. Forest habitat types of central Idaho. USDA Forest Service Gen. Tech. Rep. INT-114.

Strong, D. R. 1986. Density vagueness: Abiding the variance in demography of real populations. Pages 257-268. in J. R. Diamond and T. J. Case. eds. Community ecology. Harper and Row, N. Y.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Wallin, K. and M. Andersson. 1981. Adult nomadism in Tengmalm's owl Aegolius funereus. Ornis Scand. 12:125-126.

Wartenberg, D., S. Ferson, and F. J. Rohlf. 1987. Putting things in order: a critique of detrended correspondence analysis. Am. Nat. 129:434-448.

White, G. C., D. R. Anderson, K. P. Burnham and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Lab.

Wiens, J. A. 1985. Habitat selection in variable environments: Shrubsteppe birds. Pages 227-252. in M. L. Cody. ed. Habitat selection in birds. Academic Press, N. Y.

Williams, D. F. and S. E. Braun. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. J. Wildl. Manage. 47:841-845.

Williams, O. 1959. Food habits of the deer mouse. J. Mammol. 40:415-419.

FIGURE LEGENDS

Figure 1. Relationships among 4 vegetation cover types as defined by principal components analysis of 21 forest structure variables. Each plot depicts the placement of 101 random plots on 2 gradients defined by PCA. **A**--PC1 on y-axis, PC2 on x-axis; **B**--PC3 on y-axis, PC4 on x-axis; **C**--PC5 on y-axis, PC6 on x-axis.

Figure 2. Relationships among 4 vegetation cover types and boreal owl nest sites as defined by principal components analysis 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**--PC1 on y-axis, PC2 on x-axis; **B**--PC3 on y-axis, PC4 on x-axis; **C**--PC5 on y-axis, PC6 on x-axis.

Figure 3. Movement pattern of 2 boreal owls from relocations of daytime roosts every 3-4 days during one season at Chamberlain Basin. **A**--Boreal 96 summer movements in 1987. **B**--Boreal 76 winter movements in 1987.

Figure 4. Seasonal 95% utilization distributions of 2 male boreal owls in Chamberlain Basin. **A**--Boreal 97 summer home range showing the low elevation nest site on the edge of its home range. **B**--Boreal 96 summer home range showing the higher elevation nest site near center of the home range.

Figure 5. Biomass of small mammals captured during 3 years in pit traps set in 7 vegetation types at Chamberlain Basin. Three sites were trapped in each vegetation type.

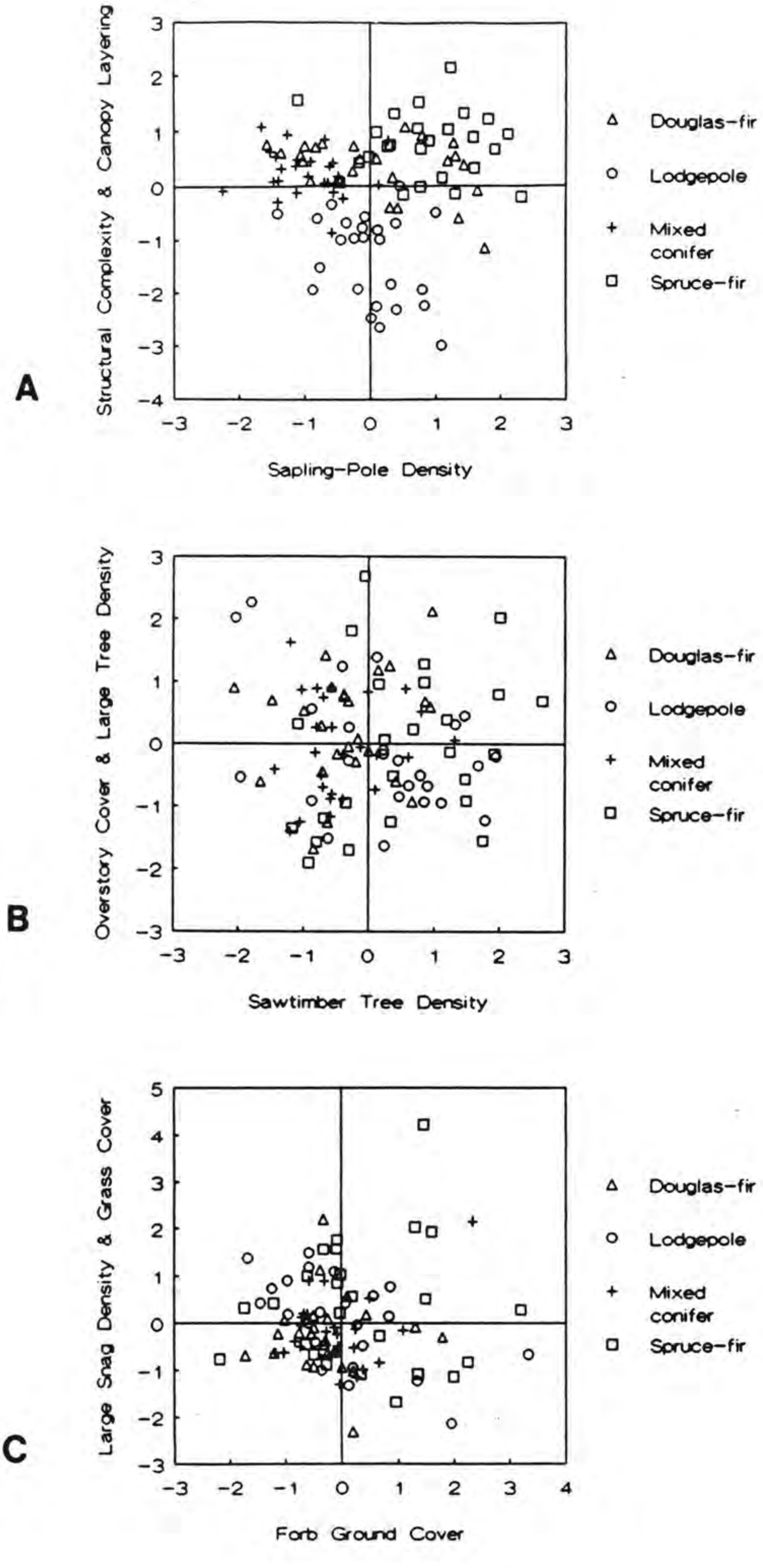
A
Structural Complexity & Canopy Layering
3
2
1
0
−1
−2
−3
−4
−3
−2
−1
0
1
2
3
Sapling-Pole Density
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir
B
Overstory Cover & Large Tree Density
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3
Sawtimber Tree Density
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir
C
Large Snag Density & Grass Cover
5
4
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3
4
Forb Ground Cover
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir

Figure 1.

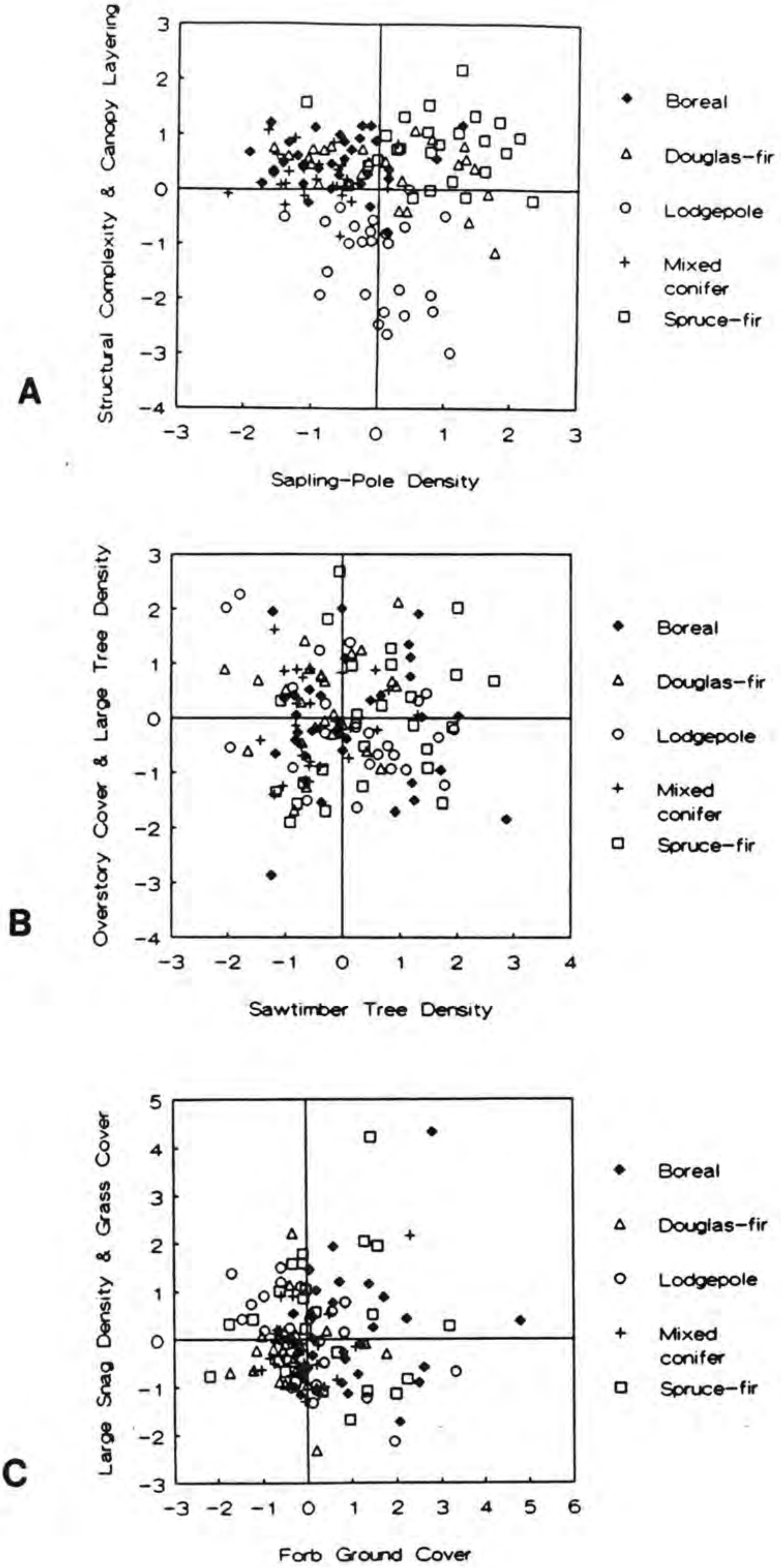
A
Structural Complexity & Canopy Layering
3
2
1
0
−1
−2
−3
−4
−3
−2
−1
0
1
2
3
Sapling-Pole Density
◆ Boreal
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir
B
Overstory Cover & Large Tree Density
3
2
1
0
−1
−2
−3
−4
−3
−2
−1
0
1
2
3
4
Sawtimber Tree Density
◆ Boreal
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir
C
Large Snag Density & Grass Cover
5
4
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3
4
5
6
Forb Ground Cover
◆ Boreal
△ Douglas-fir
○ Lodgepole
+ Mixed conifer
□ Spruce-fir

Figure 2.

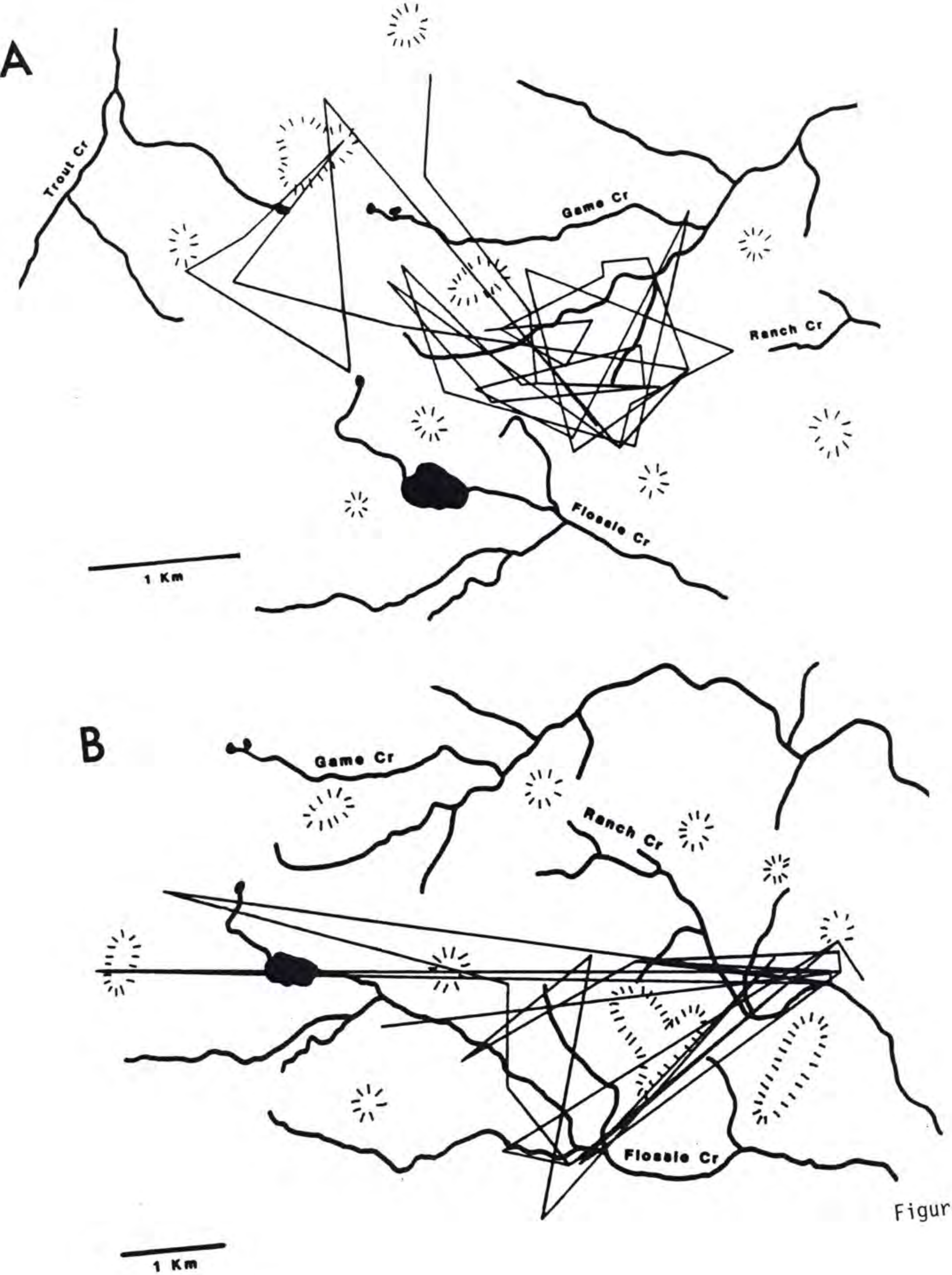
A
Trout Cr
Game Cr
Ranch Cr
Flossie Cr
1 Km
B
Game Cr
Ranch Cr
Flossie Cr
1 Km

Figure 3.

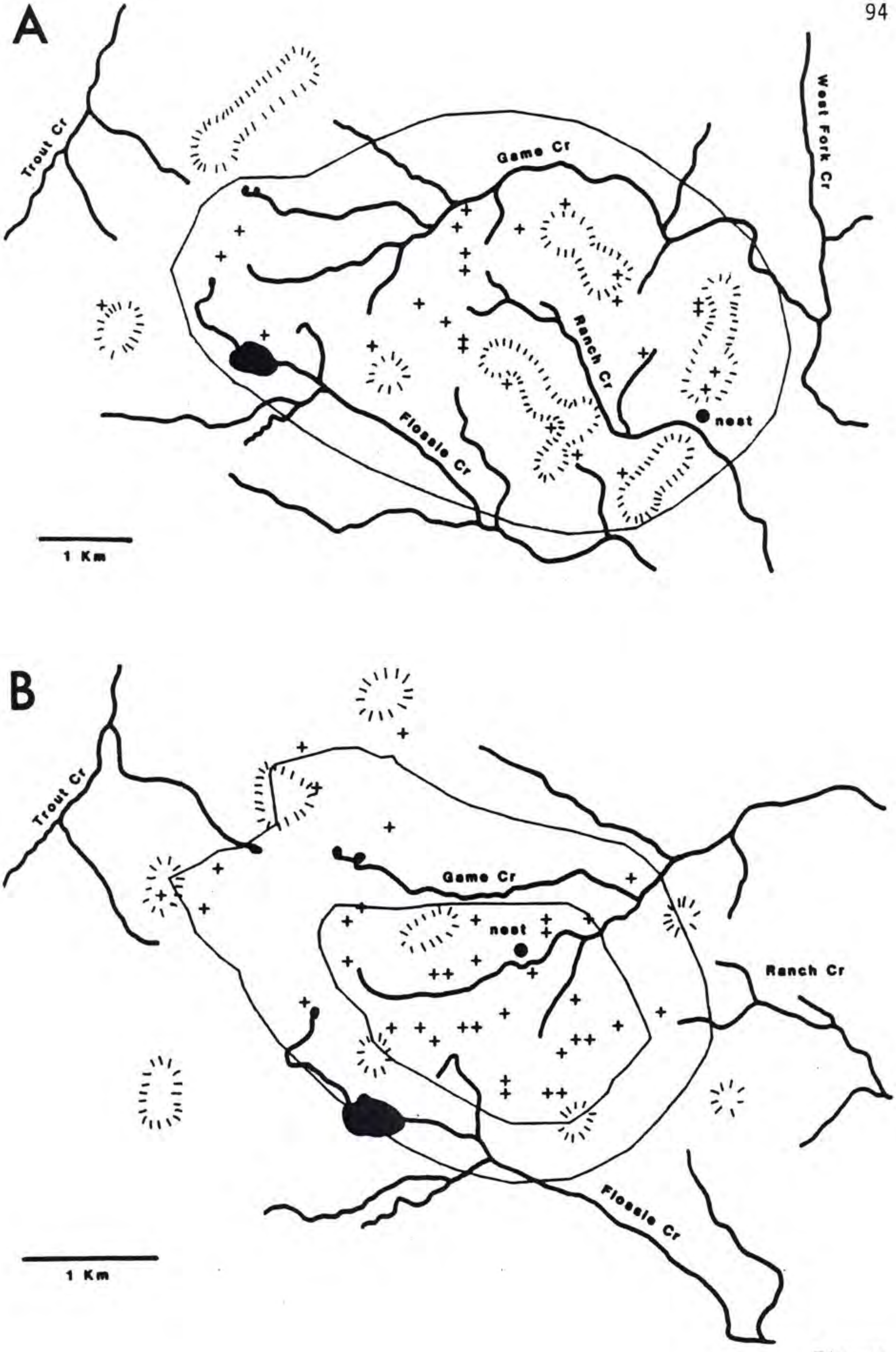
A
Trout Cr
Game Cr
West Fork Cr
Ranch Cr
Flossie Cr
nest
1 Km
B
Trout Cr
Game Cr
nest
Ranch Cr
Flossie Cr
1 Km

Figure 4.

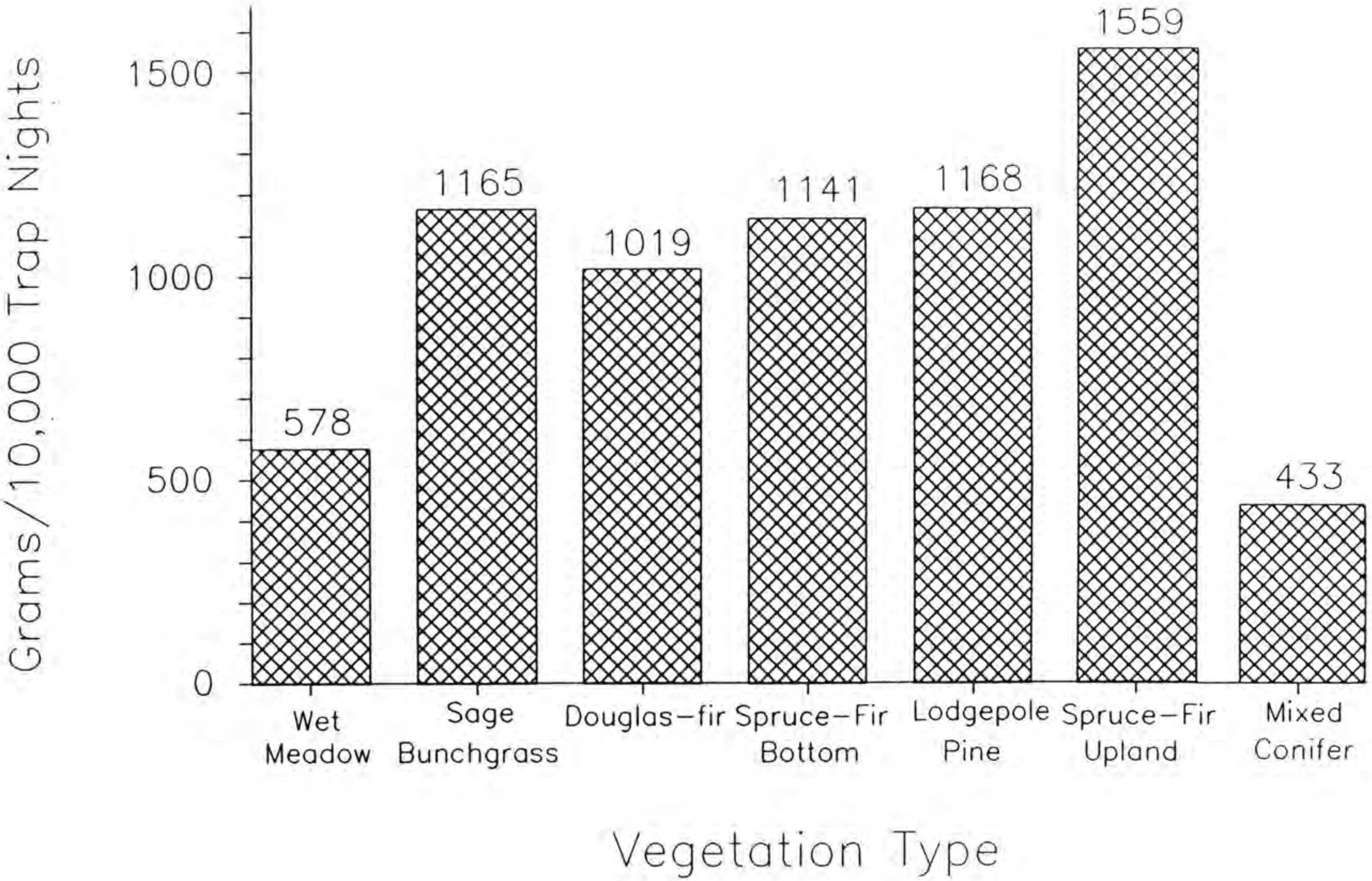
Grams/10,000 Trap Nights
0
500
1000
1500
578
1165
1019
1141
1168
1559
433
Wet Meadow
Sage Bunchgrass
Douglas-fir
Spruce-Fir Bottom
Lodgepole Pine
Spruce-Fir Upland
Mixed Conifer
Vegetation Type

Figure 5.

Table 1. Characteristics of forest structure measured at boreal owl calling sites located throughout the Northern Rockies. As described in the text, we summarized more northern, wet forests (Maritime) separately from southern, dryer sites (Continental). Canopy cover is recorded in layers above ground.

	Maritime (N=12)			Continental (N=9)		
Stuctural Feature	Mean(± 95% Bound)	Range	C.V.(%)	Mean(± 95% Bound)	Range	C.V.(%)
Tree Density (No/ha)						
2.5-7.6 cm dbh	740(476.5)	30-2543	102	387(164.7)	150-793	56
7.6-15 cm dbh	298(149.7)	15-853	80	284(59.7)	164-419	28
15-23 cm dbh	101(52.3)	0-314	82	204(104.6)	75-478	68
23-38 cm dbh	131(54.2)	45-329	66	176(87.5)	0-374	66
38-53 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(19.9)	0-80	205
Basal Area (m^2/ha)						
Trees >30.5 cm dbh	29.7(11.35)	7.3-68.5	61	14.7(6.57)	3.7-34.2	59
Conifer Canopy Cover by Canopy Layer (%)						
0-1 m	16(3.8)	4-37	52	8(6.3)	0-21	107
1-2 m	16(3.2)	5-33	47	8(4.5)	1-17	75
2-4 m	19(2.6)	8-34	32	12(5.4)	2-22	57
4-8 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 (%)						
0-1 m	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

Table 2. Structural characteristics of four forest vegetation types measured on 25 randomly selected macroplots for each vegetation type. Vegetations were defined by dominant overstory trees. Values recorded are means with 95% bounds in parentheses.

Structural Feature	Forest Type			
	Lodgepole	Mixed Conifer	Douglas-Fir	Spruce-Fir
Vegetation Cover by Canopy Layer (%)				
0-1 m	2(1.2)	3(0.7)	6(1.4)	16(3.5)
1-2 m	2(1.3)	6(1.3)	10(1.5)	15(3.0)
2-4 m	5(1.8)	12(2.5)	16(2.7)	19(2.5)
4-8 m	13(3.7)	25(4.0)	28(3.5)	25(3.1)
>8	33(4.9)	30(4.1)	32(5.0)	30(5.6)
Shrub Canopy Cover (%)				
0-1 m	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)	1040(361.5)	935(212.4)
7.6-15 cm dbh	284 (54.5)	255 (72.2)	443(171.6)	530(115.3)
15-23 cm dbh	204 (95.4)	147 (40.6)	178 (30.1)	337 (79.4)
23-38 cm dbh	176 (79.9)	77 (24.2)	111 (25.6)	193 (34.2)
38-53 cm dbh	4 (4.0)	17 (5.5)	28 (13.6)	32 (10.1)
>53 cm dbh		25 (6.6)	16 (5.4)	12 (.4)
2.5-38 cm dbh snags	111 (74.7)	73 (30.1)	211(136.8)	194 (31.5)
>38 cm dbh snags		7 (6.4)	2 (1.4)	12 (8.3)
Basal Area (m^2/ha)				
Trees >30.5 cm dbh	2.0(1.0)	15.8(2.8)	12.7(3.5)	13.1(4.01)

Table 3. Pattern matrix for 6 Principal Components derived from analysis of structural features measured at 101 random plots in four general vegetation types at Chamberlain Basin. 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 7.6-15 cm dbh	-0.733	0.481				
Density Trees 15-23 cm dbh	-0.513			0.501		
Density Trees 23-38 cm dbh				0.722		
Density Trees 38-53 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 1-2 m	0.666	0.607				
Conifer Cover 2-4 m	0.763					
Conifer Cover 4-8 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
Eigen Value	5.839	3.771	2.037	1.743	1.223	1.104
Percent of Variance Explained	27.8	18.0	9.7	8.3	6.1	5.3
Cumulative Percent	27.8	45.8	55.5	63.8	69.9	75.2

Table 4. Characteristics of forest structure measured at 33 boreal owl calling sites in the RNRW. Canopy cover is recorded in layers above the ground.

Structural Feature	Mean(±95% Bound)	Range	C.V.(%)
Tree Density (No/ha)			
2.5-7.6 cm dbh	450 (140)	29-1795	91
7.6-15 cm dbh	298 (86)	82-1226	85
15-23 cm dbh	162 (40)	15- 434	72
23-38 cm dbh	126 (31)	15- 320	72
38-53 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^2/ha)			
Trees >30.5 cm dbh	17.8 (3.1)	3.7- 40.9	51
Conifer Canopy Cover by Canopy Layer (%)			
0-1 m	6 (1.7)	1-21	84
1-2 m	8 (1.3)	1-16	47
2-4 m	13 (2.1)	5-27	47
4-8 m	22 (3.2)	2-41	43
>8 m	30 (4.3)	4-56	42
Ground Cover (%)			
Forb	12 (4.0)	1-55	73
Grass	8 (3.1)	4-50	50
Subshrub	7 (27.0)	0-26	111

Table 5. Forest Structure at 19 different nest trees used by boreal owls in Chamberlain Basin. Tree densities are reported for two concentric circular plots, an inner circle 5.2 m radius and outer extending from 5.2 m to 11.4 m.

Site Characteristic	Mean	± 95% Bound
Tree Density (No/ha)		
Inner Plot		
2.5-7.6 cm dbh	174	111.9
7.6-15 cm dbh	98	48.1
15-23 cm dbh	114	60.1
23-38 cm dbh	136	73.7
38-68 cm dbh	60	42.5
> 68 cm dbh	11	15.6
Tree Density (No/ha)		
Outer Plot		
2.5-7.6 cm dbh	242	107.3
7.6-15 cm dbh	178	70.1
15-23 cm dbh	124	49.5
23-38 cm dbh	130	56.6
38-68 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^2ha)	33.7	3.62
Canopy Cover (%)	55	7.7
Topographic Features		
Distance to Water (m)	201	98.9
Slope (%)	28	5.8

Table 6. Habitat types (Steele et al. 1981) of 194 winter and 342 summer roost sites used by boreal owls at Chamberlain Basin. We combined rare habitats with types of similar moisture and structural characteristics.

Habitat Type	No. of roosts (%)	
	Winter	Summer
Douglas-fir Huckleberry (Psme/Vagl)	4(2.1)	3(0.9)
Douglas-fir PineGrass (Psme/Caru)[1]	45(23.2)	6(1.7)
Subalpine-fir Twisted Stalk (Abla/Stam)[2]	12(6.2)	16(4.7)
Subalpine-fir Dwarf Huckleberry (Abla/Vaca)[3]	25(12.9)	2(0.9)
Subalpine-fir Twinflower (Abla/Libo)	9(4.6)	5(1.5)
Subalpine-fir Bear Grass (Abla/Xete)[4]	63(32.5)	286(83.4)
Subalpine-fir Grouse Whortleberry (Abla/Vasc)[5]	11(5.67)	12(3.5)
Subalpine-fir Pine Grass (Abla/Carv)	25(12.9)	12(3.5)

[1] Represents sum of Psme/Carv, Psme/Syal, Psme/Spbe, Psme/Bere sites. These are generally sites of mixed Douglas fir and Ponderosa pine overstory.

[2] Represents sum of Abla/Stam, Abla,Caca, and Abla/Cabi sites - hydric stands with lush understory.

[3] Represents sum of Abla/Vaca, Psme/Vaca sites - low elevation cold air drainage.

[4] Represents sum of Abla/Xete, Abla/Alsi, Abla/Vagl, Abla/Spbe, and Abla/Mefe -- high elevation mesic sites.

[5] Represents sum of Abla/Vasc, Abla/Cage, and Abla/Arco - more harsh sites than beargrass sites.

Table 7. Seasonal boreal owl roost characteristics; Mean(± 95% bound). Tree densities were sampled from two concentric circular plots around the roost site. The inner circle is 0.0084 ha and outer "donut" 0.0321 ha.

Variable	Season Winter (N=189)	 Summer (N=241)
Canopy Cover (%)	58.5(1.91)	63.5(1.54)
Basal Area (m^2/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[1]	797(120.5)	1380(142.4)
2.5-7.6 cm dhb - Outer[2]	864(119.6)	1233(98.6)
7.6-15 cm dhb - Inner	561(81.3)	897(78.8)
7.6-15 cm dhb - Outer	641(74.5)	869(66.5)
15-23 cm dbh - Inner	261(32.0)	341(33.5)
15-23 cm dbh - Outer	287(26.3)	359(23.2)
23-38 cm dbh - Inner	130(20.2)	181(21.3)
23-38 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[3]	305(53.0)	269(44.5)
15-38 cm dbh Snags	37(7.9)	49(8.8)
> 38 cm dbh Snags	2(1.2)	8(2.4)

---

[1] Inner circular plot.
[2] Outer donut.
[3] Snags measured in 0.04 ha circular plot.

Table 8. Temperature differences between roost site and a near-by opening, by temperature class.

Temperature in open (°F)	n	Mean difference	Std. Error of mean	T	*P*
30-40	80	0.13	0.08	1.69	0.10
40-50	101	0.34	0.13	2.62	0.010
50-60	99	0.71	0.17	4.13	0.0001
60-70	125	1.00	0.17	5.82	0.0001
> 70	80	1.76	0.22	7.93	0.0001

Table 9. Seasonal home range size (ha) for boreal owls at Chamberlain Basin. Areas are 95% utilization distributions. Sample size is in parenthesis.

			Home RangeArea		
Year	Owl	Sex	Winter	Summer	Combined
1984	33	M			814 (13)
	34	F	320 (10)		607 (20)
	37	F	1504 (16)		4127 (24)
	42	M		610 (16)	1166 (24)
1985	43	M	1411 (19)	530 (14)	2341 (33)
	76	M	1282 (24)	229 (19)	2581 (43)
	77	M	2359 (31)	1265 (14)	2360 (45)
	84	M	946 (12)	1421 (17)	2141 (29)
1986	95	F	1832 (12)		
	96	M		1100 (53)	1438 (58)
	97	M	2001 (13)	2386 (27)	6876 (40)
	55	F		1448 (40)	
1987	96	M	261 (21)	797 (37)	911 (58)
	76	M	2259 (28)	1520 (45)	1761 (73)
	104	M	473 (22)	884 (38)	1019 (60)
	105	F	826 (17)	747 (21)	1122 (38)
	107	F	3390 (30)	2037 (17)	3517 (47)
	117	M		1884 (20)	1161 (26)
	133	F		874 (18)	

Table 10. Diet of boreal owls at Chamberlain Basin Idaho estimated from pellets, cached prey, and nest contents of 31 owls in 1981 and 1984-1988.

	Percent Frequency							
	Winter			Summer			Year-Round	
	Male	Female	Total	Male	Female	Total	Freq(%)	Biomass(%)
Mammals								
N. red-backed vole	49	49	49	34	13	31	36	34
N. pocket gopher	8	6	7	10	16	11	10	32
Sorex spp.	15	6	12	11	10	11	11	2
Microtus spp.	12	7	11	8	12	8	9	10
Deer mouse	6	10	7	5	5	5	6	5
Heather vole	2	0	2	5	2	4	4	3
N. Flying squirrel	1	14	5	0	tr	tr	1	6
Yellow-pine chipmunk	2	0	1	2	2	2	2	3
Jummping mouse	0	0	0	3	0	2	2	1
Pica	0	0	0	tr	1	tr	tr	1
Woodrat spp.	0	0	0	0	1	tr	tr	tr
Weasel spp.	0	1	tr	0	0	0	tr	tr
Water vole[1]	0	0	tr	0	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	26162

[1] *Microtus arvicola*

Table 10. Diet of boreal owls at Chamberlain Basin Idaho estimated from pellets, cached prey, and nest contents of 31 owls in 1981 and 1984-1988.

	Percent Frequency							
	Winter			Summer			Year-Round	
	Male	Female	Total	Male	Female	Total	Freq(%)	Biomass(%)
Mammals								
N. red-backed vole	49	49	49	34	13	31	36	34
N. pocket gopher	8	6	7	10	16	11	10	32
Sorex spp.	15	6	12	11	10	11	11	2
Microtus spp.	12	7	11	8	12	8	9	10
Deer mouse	6	10	7	5	5	5	6	5
Heather vole	2	0	2	5	2	4	4	3
N. Flying squirrel	1	14	5	0	tr	tr	1	6
Yellow-pine chipmunk	2	0	1	2	2	2	2	3
Jummping mouse	0	0	0	3	0	2	2	1
Pica	0	0	0	tr	1	tr	tr	1
Woodrat spp.	0	0	0	0	1	tr	tr	tr
Weasel spp.	0	1	tr	0	0	0	tr	tr
Microtus arvicola	0	0	tr	0	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	26162

Table 11. Mean weight of small mammals used to calculate biomass of prey consumed by boreal owls. Pocket gopher and flying squirrel values from Hall (1946). Otherwise all values result from trapping in Chamberlain Basin.

Species	Age	Weight(g)	95% Bound(g)	Sample Size
Red-backed Vole	Adult	26.5	0.74	100
Red-backed Vole	Juv.	12.2	0.67	48
Deer Mouse	Adult	24.2	1.15	32
Deer Mouse	Juv.	11.5	2.16	6
Heather Vole	Adult	22.7	3.47	9
Heather Vole	Juv.	13.8	5.01	3
Microtus spp.	Adult	30.0	3.01	12
Microtus spp.	Juv.	12.2	2.11	9
Sorex spp.		6.1	0.58	18
Chipmunk		50.8	2.30	24
Pocket Gopher		101.2		
Flying Squirrel		140		

Table 12. Trend in boreal owl surveys from 1984-1987 at Chamberlain Basin.

	Survey Period			
	1984 18 Jan-23 April	1985[1] 25 Jan-2 May	1986 14 Jan-7 May	1987 16 Feb-27 April
No. Surveys	13	29	32	36(5)[2]
No. listening nights	5	16	5	19(0)
Kilometers surveyed	64	195	217	218(30)
% surveying or trapping nights males heard	56	51	8	49(60)
% surveying nights calling males heard	62	48	6	53(60)
# calling males heard per survey km	0.24	0.07	0.02	0.14(0.10)
# owls captured				
winter	9	5	3	7
year	9	6	4	8

---

[1] Four people worked in 1985 and 1987; two people in 1984 and 1986.

[2] Numbers in parenthesis represent results of surveys at Arctic point-Hotsprings Meadows

Table 13. Trend in boreal owl surveys from 1984-1986 at Cold Meadows.

	Survey Periods		
	1984 19 Feb-4 Mar 3 Apr-11 April	1985 25 Feb-7 Mar 6 Apr-18 Apr	1986 27 Mar-11 Apr
# Surveys	17	20	11
Kilometers surveyed	74	100	70
% surveying nights calling males heard	40	20	18
# calling males heard per km survey	0.20	0.07	0.09

Table 14. 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 (Korpimaki 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 June	7-12 July	?	Youngest 1 day
	55	?	14 May	14 June[1]	15 July	4-6 July	3rd egg laid
	58	18 April	7 May	5 June	2-8 July	22-26 July	Youngest 1 day
1985	86	23 April	15 May	13 June	15 July	5 July	Youngest 1 day
	87	?	20 May	18 June			Youngest 2 day
1986	95	18 April	by 30 April[2]				
	55	?	24 May	22 June			During laying
1987	105	13-14 April	21 April	20 May	16-18 June	9 June	Youngest 2 days
	107	16 April[3]					
	107	26-30 April	1 May	29 May			Youngest 4 days
	115	?	12 April	11 May			Youngest 12 days
	128	16 April[4]					
	133	?	17 April	16 May	14-15 June	6 June	Youngest 6 days
1988	134	?	14 April	13 May			Unhatched egg
	135	?	17 April	18 May			2 unhatched eggs

[1] 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 two days (between the second and third egg) which likely accounts for the long incubation period.

[2] Female abandoned the nest on 30 April without being disturbed and two eggs had been laid.

[3] Female abandoned her first nest due to disturbance and initiated a second nest by 30 April.

[4] Female was killed by a predator away from the nest before laying.

Table 15. Relationships (Spearman Rank Correlation) between small mammal capture rate and forest structure measured at 14 pit trap sites. Principal component scores describing six gradients of forest structure were determined from analysis of 101 forest sites including the 14 trapping locations. Significant correlations are highlighted (*$P \le 0.10$, ** $P \le 0.05$).

	Principal Component					
Species	1	2	3	4	5	6
Red-backed vole	0.608**	0.377	0.079	-0.141	0.454	0.060
Shrew spp.	0.552**	0.108	-0.103	-0.486*	0.793	0.178
Deer Mouse	-0.007	0.119	-0.181	-0.449	0.181	-0.240
Chipmunk	-0.581**	-0.681**	0.210	0.245	-0.357	0.014

Table 16. Frequency of capture for 7 species of small mammal in 9x10 grid of snap traps at Chamberlain Basin. 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. Table shows number of adults captured with juveniles in parenthesis.

Small Mammal Species	Sage (4 yrs)	Wet Meadow (3 yrs)	Lodgepole 1* (4 yrs)	Lodgepole 2** (3 yrs)	Douglas Fir (4 yrs)	Mixed Conifer (5 yrs)	Spruce Fir (2 yrs)
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)
Sorex ssp	0	16	4	1	0	1	71
Microtus spp	7(2)	5(5)	0(0)	0(0)	0(0)	0(0)	0(0)
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)
Chipmunk	18(0)	1(0)	3(0)	4(0)	1(0)	4(0)	0(0)

*Lodgepole pine forest with lush understory vegetation and some downed logs.

**Lodgepole pine forest with dry understory and no downed logs.