

RESOURCE PARTITIONING AMONG
SIX FOREST OWLS IN THE RIVER
OF NO RETURN WILDERNESS, IDAHO

By

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RESOURCE PARTITIONING AMONG
SIX FOREST OWLS
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by
Gregory Dale Hayward

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ABSTRACT

I studied resource partitioning among the forest owls in the River of No Return Wilderness, Idaho, during the winter and spring of 1980 and 1981. Recorded calls were broadcast to locate owls during late winter. Habitats used were characterized according to vegetation structure at the singing location (microhabitat) and broad vegetation categories obtained from aerial photographs (macrohabitat). Individual radio-tagged saw-whet, boreal, and screech owls provided data on daily activity. Regurgitated pellets were analyzed for food habits.

Stepwise discriminant function analysis and multivariate analysis of variance were used to detect differences in the species microhabitat and macrohabitat, respectively. Information from the literature supplemented my own data to compare species' activity periods and food habits.

The four resources partitioned among species were macrohabitat, microhabitat, temporal resources, and food. The pygmy owl, a food and habitat generalist, foraged diurnally more than the other species, and took a higher proportion of birds. The flammulated owl was able to coexist within the territories of other owl species by specializing on forest moths. The saw-whet, boreal, screech, and great-horned owls, all prefer mammalian prey, but segregate through differences in

macrohabitat, microhabitat, and the size class of prey.

Screech owl distribution is limited by occurrence of deciduous riparian habitats and possibly climatic conditions. Boreal owls may be confined to high elevations by habitat availability and by competition from the abundant saw-whet and screech owls at lower elevations. Likewise, saw-whet owls are less abundant at high elevations in sympatry with boreal owls. A paucity of stick nests possibly limits distribution and abundance of great-horned and long-eared owls.

Roost sites chosen by radio-tagged boreal, saw-whet, and screech owls were examined during winter, spring, and summer to compare species roosting behaviors. Roosts used by boreal and saw-whet owls were dispersed throughout their home range. Individual screech owls often returned to preferred roost sites. The amount of protection afforded by roost sites varies among the three species. Boreal owls roosted in situations that provided less protection immediately above the bird. Saw-whet owls roosted much further from the tree bole than the other species. I propose that for the owls studied, roost sites are chosen to provide protection from predators more so than for thermal economy.

I present results of three methods of home range estimation for three saw-whet, two screech, and one boreal owl.

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CHAPTER ONE: RESOURCE PARTITIONING

Abstract: I studied resource partitioning among the forest owls in the River of No Return Wilderness, Idaho, during the winter and spring of 1980 and 1981. Of 7 owl species observed; the pygmy (Glaucidium gnoma), saw-whet (Aegolius acadicus), boreal (A. funereus), screech (O. asio macfarlanei), and great-horned (Bubo virginianus) owls were relatively abundant. Long-eared (Asio otus) and flammulated (Otus flammeolus) owls were rarely observed. Recorded calls were broadcast to locate owls during late winter. Habitats used were characterized according to vegetation structure at the singing location (microhabitat) and broad vegetation categories obtained from aerial photographs (macrohabitat). Individual radio-tagged saw-whet, boreal, and screech owls provided data on daily activity. Regurgitated pellets were analyzed for food habits.

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more than the other species, and took a higher proportion of birds. The flammulated owl was able to coexist within the territories of other owl species by specializing on forest moths. The saw-whet, boreal, screech, and great-horned owls, all prefer mammalian prey, but segregate through differences in macrohabitat, microhabitat, and the size class of prey.

Screech owl distribution is limited by occurrence of deciduous riparian habitats and possibly climatic conditions. Boreal owls may be confined to high elevations by habitat availability and by competition from the abundant saw-whet and screech owls at lower elevations. Likewise, saw-whet owls are less abundant at high elevations in sympatry with boreal owls. A paucity of stick nests possibly limits distribution and abundance of great-horned and long-eared owls.

INTRODUCTION

Ecology involves the search for repeated patterns in the structure and function of natural communities. The niche of individual species and competitive interactions among species, are fundamental components of community structure and function.

Hutchinson (1958) viewed the niche as an n-dimensional hypervolume representing the combination of factors which allow

a species to persist in a community. This model provided a conceptual framework to visualize community structure. Hutchinson (1957) incorporated species interactions into the niche concept by defining a species realized niche as a subset of its fundamental niche under the pressures of competition and predation.

The competitive exclusion principle states that two species cannot coexist on the same limiting resources or occupy the same niche. Laboratory experiments in the 1920's and 1930's supported this principle, whereas observations of natural communities were often inconsistent. Following MacArthur's pioneering work (MacArthur 1958, 1968), numerous field studies examined resource partitioning between ecologically related species (Schoener 1974). These investigations were mostly observational rather than experimental, and searched for ecological differences between species. Habitat, food, and time were the major resource dimensions addressed in studies of coexisting species (Pianka 1978).

Field studies have shown that each of the four major resource dimensions are important in separating the niches of closely related species under different circumstances. Species segregation across habitats (macrohabitat partitioning) may correspond to altitudinal zonation (Heller 1971, Noon 1980), soils (Miller 1964), or interspecific aggression (Heller 1971, Terborgh 1970, Diamond 1973, Cody and Walter 1976).

Microhabitat characteristics, especially structural features, are important in segregating birds (Balda 1975) and small mammals (Dueser and Shugart 1979). The habitat associations of birds have been studied across wide habitat gradients (James 1971, Cody 1968, Wiens and Rotenberry 1981) and intensively within single units of vegetation structure (Whitmore 1977). Niche segregation occurs at several levels, from selection for specific shrub species in shrubsteppe communities (Wiens and Rotenberry 1981), to segregation by feeding zone in eastern forest communities (MacArthur 1958).

The food niche is especially important for segregation among carnivores that feed on relatively large prey (Schoener 1974). Thus, the food niche has been emphasized over other niche dimensions in studies of raptors. Few researchers, however, have distinguished ecological segregation by food habits from segregation through foraging habitat selection (Kenward 1982).

Species may only segregate through differences in their periods of intensive resource use (temporal separation), if contested resources (i.e., food, nest site) are renewable. Segregation may occur on a seasonal or daily time schedule. Strigiformes and falconiformes appear to segregate through circadian activity patterns (Cody 1974:48). Temporal segregation between species within either group, however, is more difficult to demonstrate (Jaksic 1982). More information is needed on the circadian activity pattern and reproductive

cycles of prey species to assess competitive relationships among predator species.

Rather than demonstrating competition, observational studies, as opposed to experimental perturbations, attempt to infer the degree of competition indirectly (Schoener 1974). Recent investigations, of niche relationships have employed multivariate analysis to reduce many correlated variables to a set of uncorrelated, interpretable niche dimensions. Examples include studies by Connor and Adkisson (1977), Raphael (1981), and Carey (1981). Direct measurement of competition is not implied by these methods, although the degree of overlap between species in the measured niche space may be inferred. Knowledge of resource abundances and turnover allow one to generalize about which niche dimensions are most contested.

Guilds consist of species with similar morphologies that require similar resources (Root 1967). Guilds are presumed to represent the arenas of most intense interspecific competition and are therefore interesting subjects for the study of resource partitioning (Pianka 1978). The number of sympatric species within a guild, and similarity in their resource demands, will determine how severely any one species' population will be limited through diffuse competition (MacArthur 1972). The most similar species in any guild, often congeners, generally overlap very little in either geographic range or habitat (MacArthur 1972).

In this study, I examined resource partitioning within a

community of forest owls to identify the most highly contested resource dimensions.

Previous work on owls has dealt primarily with food habits, sensory abilities, and distribution, and has concentrated on species inhabiting open habitats or agricultural areas (bibliographies Clark et al. 1975, Knight 1979). General references (Bent 1961, Eckert and Karalus 1974) contain anecdotes on habitats 'favored' and periods of activity. Few extensive studies quantify niche relationships, or examine the structure of complete owl communities. Exceptions include early work describing the structure of an entire raptor community by Craighead and Craighead (1956), a long term study of screech owls by Van Camp (1975), Southern's (1970) comprehensive description of population regulation in English tawny owls, and Fuller's (1979) analysis of space and time niches of four raptors.

Both European (Herarra and Heraldo 1976) and North American owls (Snyder and Wiley 1976) prey predominantly on mammals. Mammals dominate the diets of 11 of 16 species in North America, and 10 of 13 European species. In the western United States most forest owls utilize small mammals as major dietary components. Percent of diet estimates are 36% for the great-horned owl (Seidensticker 1968), 82% for the long-eared owl (Marti 1976), 91% (winter) and 52% (summer) for the screech owl (Craighead and Craighead 1956), 99% for the saw-whet Owl (Spurr 1952), 88% for the boreal Owl (Norberg

1964).

Marti (1974) studied feeding niche segregation among four owl species. Although there was substantial prey overlap, prey size selection was judged to be the primary factor in feeding niche segregation. Herrera and Heraldo (1976) reported that five of seven central European owls specialized on the single genus Microtus. Dietary overlap occurs among owl species of central and northern Europe to a much greater extent than in other predatory communities (Herrera and Heraldo 1976). Lack (1946) postulated that dietary overlap is tolerable among central European owl species because prey usually are superabundant, and therefore not limiting. Herrera and Heraldo (1976) suggest that voles for example are not in short supply even in non-peak years. These authors propose that spatial segregation does not operate in northern European owl communities but suggest that information on habitat selection is needed.

These studies show that extensive food niche overlap does occur among owl species. Therefore, niche differences may occur on alternate resource dimensions. Most raptor studies presume that the high cost (time) per prey item forces predators to segregate by specializing on different foods. Each species consumes an optimum prey size. Other factors must

¹Data represent frequency in terms of numbers of prey items. All other data is percent biomass.

be considered, such as morphological adaptations related to locomotion. These characteristics limit the range of foraging habitats and techniques available to the species. Competition for limited food, therefore, can be relieved by specialization in microhabitat selection and foraging periods.

Assessment of food niche overlap among owls is difficult. Assessment of prey selection requires good estimates for both prey use and availability. Prey densities must be established for all habitats and seasons. However, knowledge of prey density does not necessarily provide an estimate of prey availability.

Prey availability is variable among species and habitats. Structural characteristics of habitat influence owl mobility and access to prey items. Therefore, a given density of Peromyscus may be differentially available to saw-whet owls in different habitats. Within the same habitat, the mice are differentially available to saw-whet and screech owls because of differences in owl morphology. The heavier screech owl may access prey beneath a dense grass mat, whereas the saw-whet owl may hunt more efficiently around shrubs or other obstacles.

Problems of prey availability assessment are compounded in winter snow. Sampling may be limited to prey occurring above snow, although owls can detect and capture prey several inches beneath the snow surface (Nero 1980). Cody (1974) identified feeding behavior and morphology as key parameters for measuring ecological isolation. Behavior determines what will be

encountered; morphology, what will be used.

In my study of several forest owls in central Idaho, I attempted to gather information on habitat, time of activity, and food, without a priori bias of how the owl niches would differ; I considered each dimension potentially important. Prior to the field work, I did not know which species bred in the study area.

STUDY AREA

The study was conducted in the River of No Return Wilderness (RNRW) of central Idaho (Fig. 1). The Wilderness consists of over 2.3 million acres of mountainous terrain on the Idaho batholith. Human impact in this roadless region has been limited to livestock grazing and local heavy disturbances associated with ranches and permanent hunting camps.

Topography of the southern portion of the wilderness consists of high mountain peaks and deep rocky canyons. A high rolling plateau, the Chamberlain Basin, dominates the north. Douglas (1964) and Hornocker (1970) describe the topography and geology of the region in more detail.

Climate varies greatly with the physiography. Lower elevations have hot, dry summers. Annual precipitation is near 40 cm along the lower stretches of Big Creek. Snow

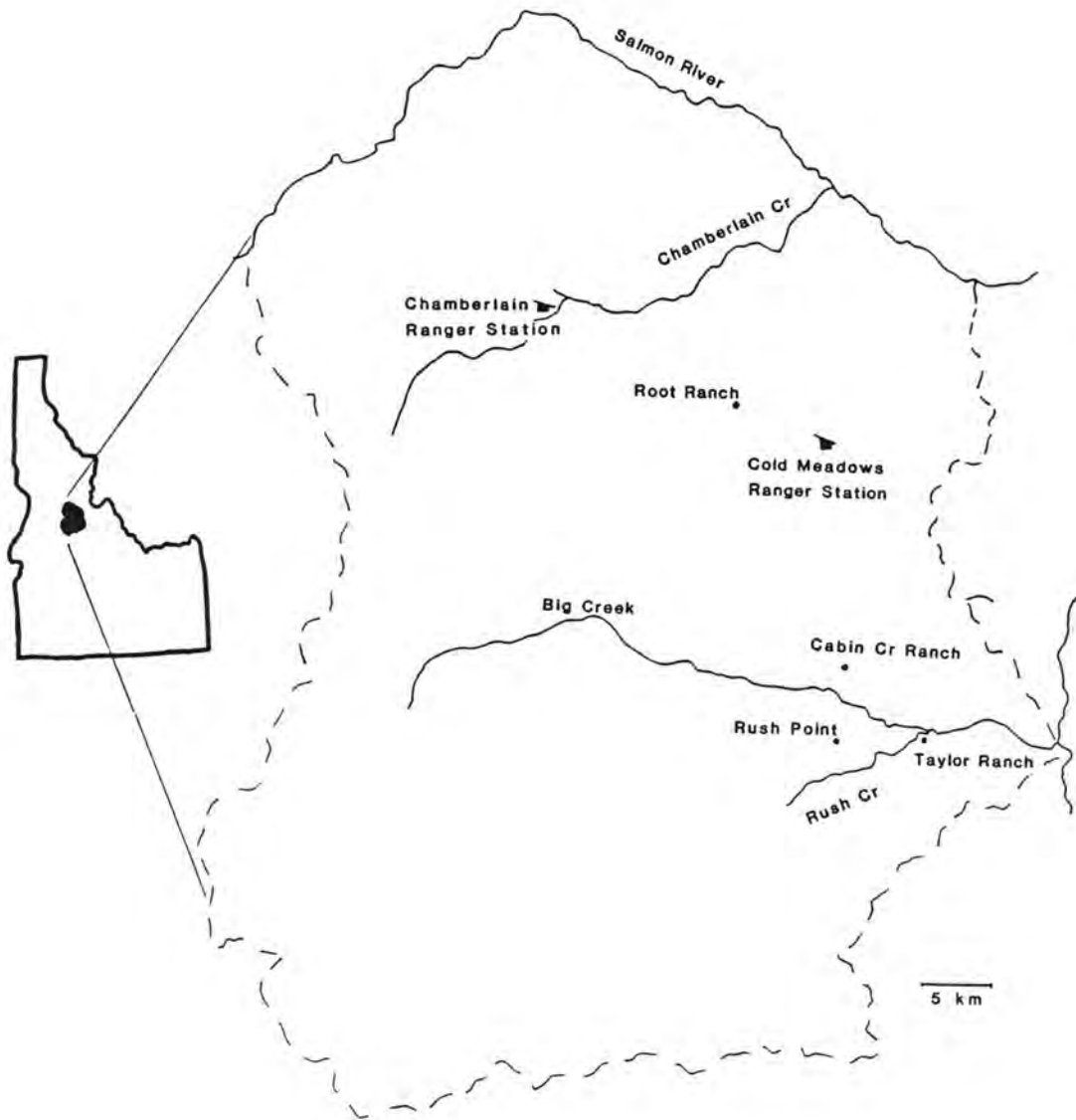


Fig. 1. Location of Taylor Ranch, Rush Point, and Chamberlain Basin study sites in the Big Creek Ranger District, Payette National Forest, Idaho.

accumulation of 16 to 46 cm occurs from late November to April at lower elevations. The high ridges and Chamberlain Basin experience cooler summers and cold winters. Snow depths reach 88 cm, and snow cover lasts from November to May.

Three study camps were established (Fig. 1) to facilitate sampling of a wide range of elevations and the diversity of vegetation, topography and climate. The Taylor Ranch and Rush Point camps were located in the rugged Big Creek canyon at elevations of 1175 m (3855 ft) and 2195 m (7200 ft) respectively. These two camps are collectively referred to as the Taylor Ranch site. The Chamberlain Basin camp was located in the plateau area at 1722 m (5650 ft) elevation.

Douglas (1964), Hornocker (1970), and Claar (1973) described the vegetation of the Wilderness Area. Douglas-fir - ninebark and Douglas-fir - Calamagrostis habitat types dominate the moist aspects in both the Rush Point and Taylor Ranch vicinities. Drier aspects support bunch grass (Agropyron spicatum and Festuca idahoensis) on the deeper soils and mountain shrubs (Artemisia tridentata, Cercocarpus ledifolius, and Purshia tridentata) on rocky soils. Topographic features of the Big Creek drainage provide a mosaic of forested and unforested habitats. Riparian habitats support Douglas-fir (Pseudotsuga menziesii) and deciduous trees including birch (Betula occidentalis), alder (Alnus tenuifolia), hawthorn (Crataegus), and scattered black cottonwood (Populus trichocarpa).

The Chamberlain Basin is dominated by evenage lodgepole pine (Pinus contorta) stands interspersed with mountain meadows. Willow carrs border some stream courses. Dry south slopes support stands of bunchgrass or sagebrush. Uneven-aged stands of mixed Ponderosa pine (Pinus ponderosa), Douglas-fir, and lodgepole pine occupy the southern aspects of more gentle slopes. These stands vary from large (>65 cm dbh), open Ponderosa pine to dense stands of regeneration and oldgrowth timber.

The relative proportions of habitats categories at the Chamberlain and the combined Rush Point and Taylor study sites were obtained from (1:15,800) color aerial photographs (Table 1).

METHODS

Locating owls

I broadcasted tape recorded owl calls from 25 January to 8 May 1980 and from 19 January to 15 May 1981 to locate owls. The Taylor Ranch, Rush Point, and Chamberlain Basin vicinities were each surveyed for approximately 10 day periods distributed throughout the census period. Survey routes were selected to allow sampling of all habitats and topographic positions at

Table 1. Relative proportion of vegetation cover types at two study sites in the River of No Return Wilderness, Idaho. Types representing less than 1% of the area are not listed.

Vegetation Type	Percent Cover	
	Taylor	Chamberlain
Douglas fir	23	
Dense Douglas fir	26	
Open lodgepole pine		36
Dense lodgepole pine		32
Mixed conifer		6
Dense mixed conifer		14
Savanna	8	
Deciduous bottom	2	
Riparian	2	4
Dry shrub	19	2
Mountain grass		4
Bunch grass	17	2
Rock	3	

each study site. Six routes at both Taylor and Chamberlain and four at Rush were surveyed an average of eight times each year (range 4-9). Total distances surveyed at the three areas were 19.2 km, 7.3 km, and 36.3 km respectively. Surveys were conducted evenings after dark and mornings before sun-up on foot or skies. I paused every 0.3 to 0.6 km to broadcast calls of one to three owl species for 3 to 5 minutes each in 15 to 30 second segments. Whenever an owl responded, the site was flagged for relocation and noted on aerial photos and 1:24,000 topographic maps. Distant owls were approached for more positive location.

On several occasions I was approached by territorial owls when I played the call. I am confident, however, that the majority of locations represent preferred singing locations within heavily used portions of the owl territories. Many owls located one night, were subsequently heard singing from the same locations when no call was played. Forty-eight percent of the owls located at Taylor and Chamberlain in 1981 were heard on more than one occasion. In the case of boreal owls Bondrup-Nielsen (1978) found the nest tree within 12 m of the favorite singing tree for all 12 nests, demonstrating the significance of the singing location.

Vegetation Sampling

The vegetation structure of each owl use area was sampled the following summer. Cover of trees, shrubs, and herbs was estimated on a macroplot established in homogeneous vegetation around the singing location. Vegetation variables and sampling methods were selected to quantify stand structural characteristics that potentially influence owl maneuverability, access to prey, and suitability of the stand for prey.

Eight, 30.5 m parallel transects were established perpendicular to the slope. Transects were randomly spaced from 6 to 20 m apart (Fig. 2). Intercept measurements along these transects provided tree and shrub cover estimates for five height categories (0-1 m, 1-2 m, 2-4 m, 4-8 m, and > 8 m). I held a 3 m rod vertically as I walked the line transect to facilitate estimation of vegetation height and cover. I recorded the number of trees in five diameter classes (1-3 in, 3-6 in, 6-9 in, 9-15 in, and > 15 in) within two, 100m² (0.02 acre) circular plots per transect. Cover of forbs, turf grasses and bunchgrasses was recorded separately on five, 0.1 m² rectangular plots (Daubenmire 1959) systematically located along each transect. I characterized vegetation structure on each site by computing averages for canopy cover by height category, timber density by diameter class, and herbaceous cover by vegetation class (Table 2).

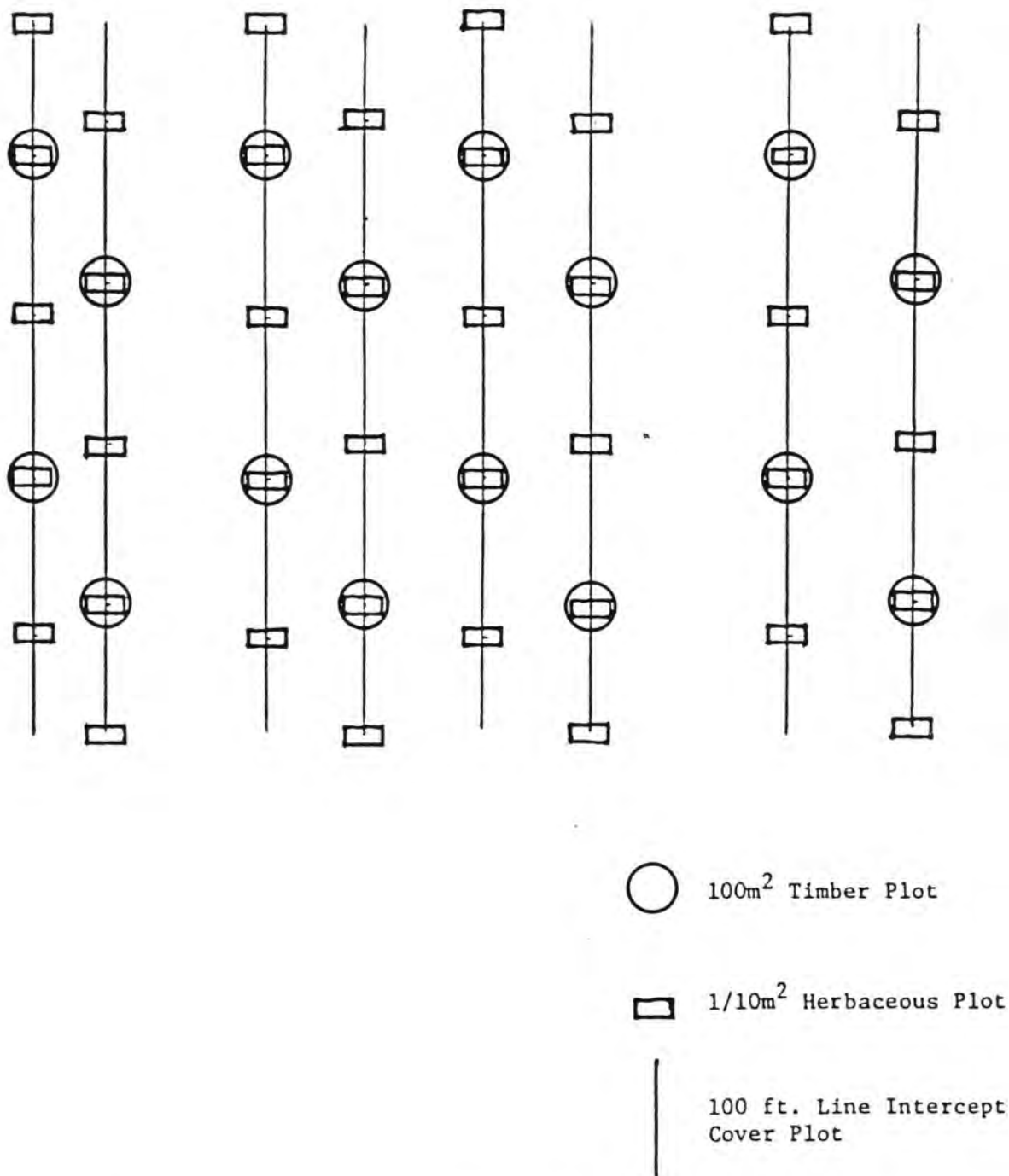


Fig. 2. Arrangement of line intercept transects, timber measurement plots, and aerial plots for measuring herbaceous cover. Both timber and herbaceous plots are placed systematically on randomly spaced line intercept transects.

Table 2. Description of variables used to measure vegetation structure within a macroplot established in owl territories, centered on singing perch.

Mnemonic	Description	Statistic
SHRUBL	Percent deciduous shrub cover 0-1 m high	Mean of eight line intercept transects
SHRUBS	Percent deciduous shrub cover 1-2 m high	
SHRUBM	Percent deciduous shrub cover 2-4 m high	
SHRUBT	Percent deciduous shrub cover 4-8 m high	
CONL	Percent conifer cover 0-1 m high	Mean of eight line intercept transects
CONS	Percent conifer cover 1-2 m high	
CONM	Percent conifer cover 2-4 m high	
CONT	Percent conifer cover 4-8 m high	
CON	Percent conifer cover 8 m high	
DECT	Percent deciduous tree cover 4-8 m high	Mean of eight line intercept transects
DEC	Percent deciduous tree cover 8 m high	
HDIV	Measure of horizontal diversity; Standard deviation of the total percent cover of shrubs and conifers 0-4 m high	Standard deviation of eight line intercept transects
VERTHET	Measure of vertical canopy diversity; Shannon-Wiener index of total cover in five canopy layers	Diversity index of total cover in five vertical canopy layers
BUNCH	Percent bunchgrass cover	Mean of 40, 1/10 m ² rectangular plots
TURF	Percent turf grass cover	
FORB	Percent cover of forbs	
MALL	Percent total herbaceous cover	
MISSTREE	Number of 0.02 acre circular plots without any trees	Total from 16, 0.02 acre circular plots
MTH	Height of tallest trees in plot	Mean from 16, 0.02 acre circular plots
SEED	Number of trees 1-3 in DBH	Mean of 16, 0.02 acre circular plots
SAP	Number of trees 3-6 in DBH	
POLE	Number of trees 6-9 in DBH	
MATURE	Number of trees 9-15 in DBH	
OLD	Number of trees 15 in DBH	
ASPEN	Number of aspen trees	Mean of 16, 0.02 acre circular plots

Mean tree density was calculated using only those plots which had trees. A variable (MISSTREE) indicated the number of nontimbered plots within the macroplot.

Macrohabitat Vegetation Sampling

Color aerial photos (1:15,800) were used to classify vegetation of the Chamberlain and Taylor areas into eight categories on the basis of dominant vegetation cover (i.e., dense lodgepole, mountain shrub, or bunchgrass). I calculated the percent cover for each vegetation category at both study sites, and used a planimeter to estimate proportions occurring within each "owl home range".

Circular home ranges were plotted on aerial photos for all owls located in winter. The singing location was defined as the home range center. I applied Koepl et al.'s (1977) home range index to radio tracking data and incorporated information from Craighead and Craighead (1969) and Forbes and Warner (1974) to define the standard home range for each species (Table 3).

Screech owls were found only along Big Creek and radio tracking indicated their territories were elongated, oriented along the creek. A circular home range was therefore not appropriate for this species. Rather, I used a 1260 by 480 m rectangle with semicircular ends on the long axis.

Food Habits

Prey species were identified from regurgitated pellets. I collected pellets beneath roost sites that were located by

Table 3. Size of home range used for macrohabitat analysis of five owl species.

Species	Area		Radius
	ha	acre	km
Pygmy owl	78	194	0.5
Saw-whet owl	78	194	0.5
Screech owl	78	194	
Boreal owl	154	380	0.7
Great-horned owl	314	776	1.0

radio tracking. Pellets were also collected from a single boreal owl nest. Because pellets were rarely gathered from roosts used on consecutive days, it is unlikely that any two pellets contained remains from the same prey item. Therefore, whenever possible, I identified prey items even if an entire skull was not present in the pellet.

Statistical Analysis

All variables intended for parametric analysis were tested for normality and were transformed, if necessary, to improve their fit. Percentage data received arcsine square root

transformation and timber densities the square root transformation (Johnson and Wichner 1982).

A matrix of twenty-five variables for each of 84 observations on four owl species was entered into stepwise canonical discriminant analysis (Kledka 1975) to find a subset of compound variables which maximized the microhabitat differences between owl species. Values were first standardized to z-scores to eliminate distortions which result from variously scaled data (i.e., variables involving proportions and tree densities) (Aspey and Blankenship 1977). Microhabitat use by five owl species was further analysed by R-factor analysis. Data were pooled for all species and formed into a matrix of owl observations by habitat variables. R-factor analysis groups correlated habitat variables to reveal the underlying structure of the data. Through factor analysis an ordination of owl observations across the major demensions of vegetation variation is calculated. The organization of owl species along the habitat gradients calculated by factor analysis are examined without concentrating on those characteristics which maximally discriminate among species, which is the goal of discriminant analysis.

Although factor analysis assumes no underlying distribution (Johnson and Wichern 1982), results are less interpretable if observations are entered from a discontinuous gradient (Gauch 1982). To avoid this problem, separate factor analyses were examined for Chamberlain and Taylor. All

relevant vegetation structure variables were used for each analysis; twelve for Chamberlain, fourteen for Taylor. Irrelevant variables were those invariant characters, such as aspen at Taylor, which were not represented in the flora. In addition, all ground cover categories were combined to form one variable MALL. Orthogonal rotation using the varimax method was performed on the factor matrix (Kim 1975) in order to establish more meaningful relationships between the original variables and derived factors. Because minor factors may be important to a species (Johnson 1981), lesser factors were examined as well as those accounting for the majority of variance in the original data. Factor loadings below .45 were considered zero factor loadings and values greater than .55 used in factor interpretation (Comrey 1973 according to Aspey and Blankenship 1977).

I compared the vegetation cover within owl home ranges to that available within the habitat. I used Hotelling's T^2 to test for macrohabitat selection by each species (Johnson and Wichern 1982). If vegetation cover within individual home ranges of a species differs significantly from the proportions of each vegetation type available at a study site, the species appears to be choosing macrohabitat nonrandomly. The mixture of vegetation cover utilized can be compared to the available mixture using Hotelling's T^2 because the test compares two mean vectors. Differences in macrohabitat selection among the owl species were identified by multivariate analysis of variance.

RESULTS

I made 247 owl observations altogether. These included seven owl species that probably bred in the RNRW. Boreal owls (Aegolius funereus) were the most common species heard at Chamberlain, followed by great horned owls (Bubo virginianus), saw-whet owls (Aegolius acadicus), pygmy owls (Glaucidium gnoma), and flammulated owls (Otus flammeolus) respectively. Saw-whet owls were the most commonly heard species at Taylor. Great-horned owls, screech owls (Otus asio macfarlanei), pygmy owls, and long-eared owls (Asio otus) were heard to a lesser extent (Table 4).

Table 4. Number of owl use areas sampled in the River of No Return Wilderness, Idaho.

Species	Study Site		
	Chamberlain	Taylor	Total
Saw-whet owl	8	37	45
Great horned owl	9	14	23
Boreal owl	8		8
Screech owl		8	8
Pygmy owl	3	5	8
Long-eared owl		2	2
Flammulated owl	1		1

Nine owls were captured. Four saw-whet owls, three screech owls, and one boreal owl were radio-tagged.

Habitat Selection

Macrohabitat

Results of Hotelling's T^2 statistic indicate that significant differences occurred between habitats used by owls and those available to them (Table 5). Differences occurred at both Chamberlain and Taylor. In those cases where the mixture of habitats selected by a species differed significantly ($p < 0.05$) from the known proportions of available habitats, univariate t-tests indicate which habitats were overutilized or avoided. A significant F statistic for Hotelling's T^2 will protect the error probability much like a protected LSD, permitting multiple comparisons using several t-tests.

Great-horned, screech and saw-whet owls at Taylor and boreal owls at Chamberlain displayed non-random macrohabitat selection (Hotelling's T^2 , $p < 0.05$). Results of the multiple t-tests for the great-horned and saw-whet owls at Chamberlain, and pygmy owl at Taylor and Chamberlain must be interpreted cautiously. Otherwise, t-values with an absolute value greater than the tabled-t indicate specific vegetation types were selectively used (+) or avoided (-) by the species (Table 5).

Great-horned, boreal, and saw-whet owls did not show significant differences in macrohabitat use at Chamberlain

Table 5. Comparison of macrohabitat used by each species and available habitat at each study site. Hotelling's T^2 statistic indicates significant differences in overall mixture of habitats used and the mixture available. In several cases small samples prevent calculation of the statistic. Univariate Student-t tests are used to indicate those vegetation categories in which the proportion of the area in owl territories differed significantly from the proportion in the available habitat. Only significant ($p < .05$) t-values are shown.

Site	Habitat/Statistic	Species				
		Great horned	Screech	Boreal	Saw-whet	Pygmy
Taylor	Douglas fir		-4.01			
	Dense Douglas fir		-2.66		-2.49	
	Dry shrub					
	Bunch grass		2.53			
	Riparian		4.13		3.72	
	Deciduous bottom	2.54	7.35			
	Savanna				2.16	
	Rock					-4.48
	Tabled-t ($\alpha = .05$)	2.37	2.37		2.08	2.78
	Hotelling's T^2	12612.5	57315.5		50.4	small sample
	F	257.40	1169.70		5.15	
Prob. F	0.048	0.023		0.004		
Chamberlain	Open lodgepole			-2.61		
	Dense lodgepole					
	Open mixed conifer					
	Dense mixed conifer					
	Dry shrub					
	Bunch grass	2.79		-3.61		
	Mountain grass					
	Riparian	4.84			2.58	
	Tabled-t ($\alpha = .05$)	2.78		2.31	2.31	12.76
	Hotelling's T^2	small sample		370147.0	40.1	small sample
	F			13219.50	1.43	
Prob. F			0.00007	0.47		

(Multivariate ANOVA Table 6). Greater macrohabitat segregation occurred in the more heterogeneous environment at Taylor as indicated by highly significant F values ($p < 0.01$) on all three measures of multivariate significance (Table 7). Disproportionate use of deciduous bottoms by screech owls is most responsible for this significant F (Table 7). This finding resulted from univariate ANOVA and significant-difference multiple-comparisons (Ott 1977) conducted on each vegetation type. Screech owl home ranges also included a higher proportion of bunchgrass habitat than other owls. This difference is expected since bunchgrass habitats were often adjacent to riverbottoms on southern exposures.

Macrohabitat specialization was further explored by examining the variety of vegetations used by each species. Niche breadth may be visualized as the degree of intersection between the frequency distribution of available resources and that for utilization. A specialist, by definition, chooses resources in disproportion to their availability; or the frequency distribution of used and available resources are dissimilar (Feinsinger et al. 1981). Niche breadth, as calculated by Feinsinger et al. (1981), for owls at Chamberlain and Taylor are shown in Table 8. I measured macrohabitat use as the proportion of the area within an owl's home range covered by a particular vegetation. The home range being a standard circle around owl locations as described under Methods. By this method, some habitats which are not used, are

Table 6. Multivariate analysis of variance testing differences in macro-habitat selected by three owl species at Chamberlain. Least significant difference is used for multiple comparisons. Under-scored species are not significantly different ($\alpha = .05$). GH=Great horned owl (N=5), BO=Boreal owl (N=9), SW=Saw-whet (N=9).

Habitat	F	Prob. > F	Multiple Comparison		
Open lodgepole	0.51	0.611	<u>GH</u>	BO	SW
Mixed conifer	0.41	0.671	<u>GH</u>	BO	SW
Dense mixed conifer	0.20	0.819	<u>GH</u>	BO	SW
Dry shrub	1.22	0.317	<u>GH</u>	BO	SW
Bunch grass	2.32	0.124	<u>GH</u>	<u>SW</u>	BO
Mountain grass	0.48	0.626	<u>GH</u>	BO	SW
Riparian	2.83	0.083	<u>BO</u>	<u>GH</u>	SW

MANOVA Statistic	Value	DF	F	Prob. > F
Hotelling - Lawley Trace	2.25	14,26	2.09	0.0503
Wilk's Criterion	0.29	14,28	1.72	0.1080
Roy's Maximum Root	2.16	2,20	21.57	< 0.05

Table 7. Multivariate analysis of variance testing differences in macro-habitat selected by four owl species at Taylor. Least significant difference is used for multiple comparisons. Underscored species are not significantly different ($\alpha = .05$). GH=Great horned owl (N=8), SC=Screech owl (N=8), SW=Saw-whet owl (N=22), PY=Pygmy owl (N=5).

Habitat	F	Prob. > F	Multiple Comparison			
Douglas fir	1.27	0.298	<u>GH</u>	<u>SC</u>	SW	PY
Bunch grass	2.48	0.075	<u>SC</u>	<u>PY</u>	GH	SW
Savanna	1.11	0.358	GH	SC	SW	PY
Dry shrub	0.37	0.772	GH	SC	SW	PY
Riparian	0.87	0.465	GH	SC	SW	PY
Deciduous bottom	15.96	0.0001	<u>SC</u>	<u>GH</u>	SW	PY
Rock	2.18	0.106	<u>GH</u>	<u>SC</u>	SW	PY

MANOVA Statistic	Value	DF	F	Prob. > F
Hotelling -Lawley Trace	2.26	21,95	3.41	0.0001
Wilk's Criterion	0.25	21,95	2.75	0.0005
Roy's Maximum Root	1.95	3,95	25.41	< 0.01

Table 8. Macrohabitat niche breadth for four owl species at Chamberlain and Taylor using Feinsinger et al.'s (1980) method.

<u>Species</u>	<u>Chamberlain</u>	<u>Taylor</u>
Great horned	0.341	0.455
Screech		0.128
Boreal	0.315	
Saw-whet	0.158	0.318

considered utilized; however, preferred habitats should consistently be represented in greater proportion than their frequency in the environment.

Screech owls had a narrow niche breadth, restricting activity to the deciduous habitat in the lowest elevations at Taylor. Boreal and great-horned owls showed much wider niche breadths. Most interesting, the saw-whet owl reduced its niche breadth between Taylor and Chamberlain (Table 8). Cautious interpretation of the niche breadths is dictated by the small, unequal sample sizes.

Microhabitat

An owl's choice of a home range with a particular vegetation physiognomy should be influenced by the owl's ability to hunt most effectively in a particular vegetation structure. Multiple stepwise discriminant analysis revealed those structural features of the vegetation which maximize differences in the microhabitat chosen. In preliminary analysis, pygmy owl habitat could not be distinguished from other species as indicated by extremely low classification success. Rather than allow the pygmy owl to influence the derived canonical variates, it was removed from calculation of the functions.

Methodology and justification for applying discriminant analysis to examine resource partitioning among species in the habitat niche is clearly described by Noon (1981, p.111) and

others (Green 1971, Green 1974, Dueser and Shugart 1979). Valid application of canonical discriminant analysis to test species' segregation requires homogeneous species' variance-covariance matrices: in effect, niches of equal size and shape (Green 1974). Figure 3 demonstrates the violation of this assumption which is confirmed by rejection of the null hypothesis, H_0 = homogeneity of within group variance-covariance matrices, using Box's M statistic (Klecka 1975). Harris (1975) states that multivariate techniques are robust to violations of normality and homogeneity of variance-covariance matrices. The procedure proposed by Green (1974) is to calculate the discriminant functions and judge their significance by their ecological interpretability, and whether they provide obvious separation among two or more species consistent with the ecologic interpretation of the functions. Based upon these criteria, canonical discriminant analysis of the owl data was considered valid and results are shown in Table 9.

Three canonical variates derived from 10 habitat variables were judged significant by a chi-square test and retained for interpretation of owl habitat preferences. These variates were retained even though low eigenvalues resulted for the second and third variates. Evaluating species means on each variate indicates which structural features are most important in distinguishing one owl's habitat from another (Fig. 4).

Canonical variate I represents a gradient of deciduous

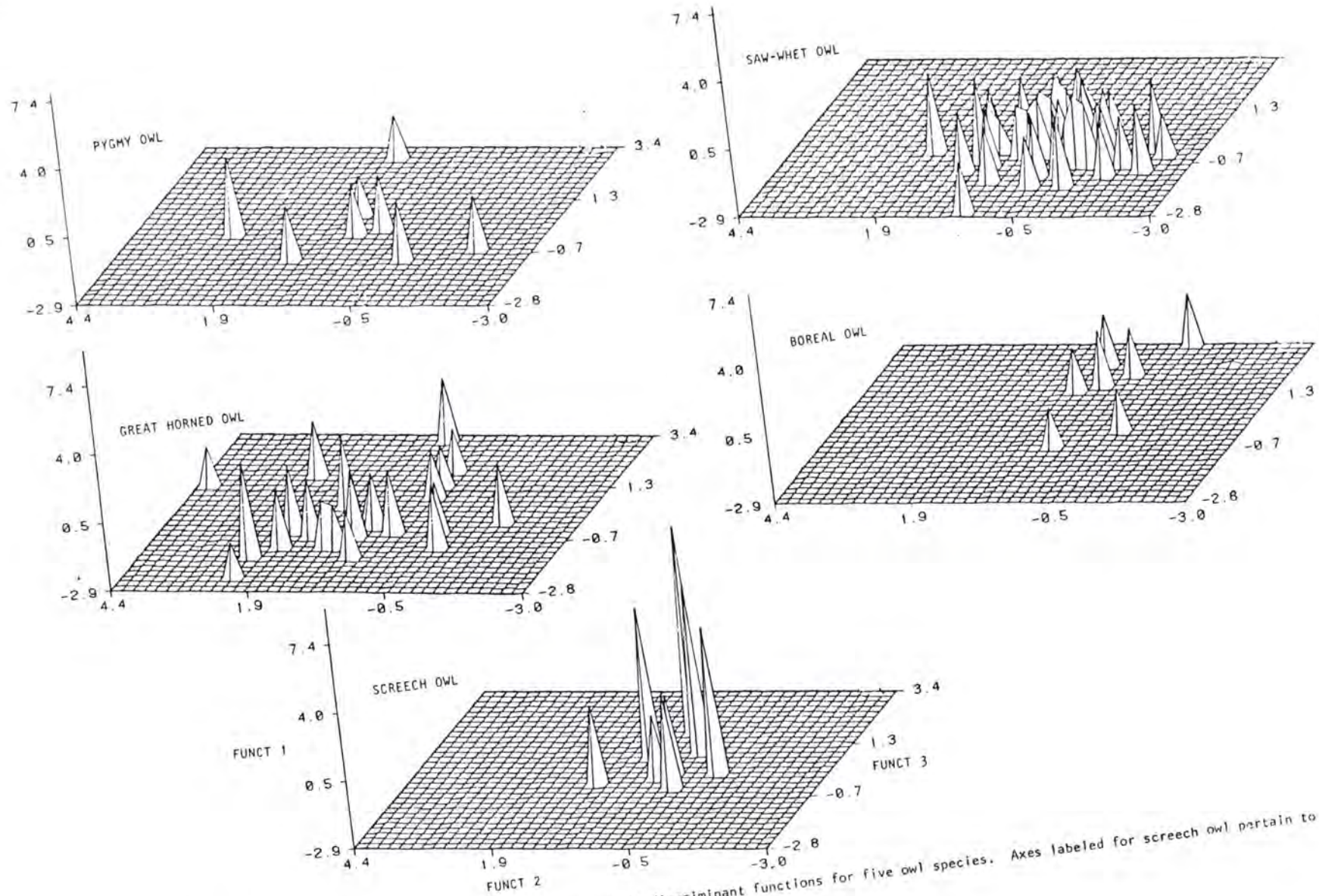


Fig. 3. Distribution of discriminant scores on three canonical discriminant functions for five owl species. Axes labeled for screech owl pertain to all species.

Table 9. Summary of multiple stepwise discriminant analysis of four owl species.

Characteristic	Canonical Discriminant Function		
	I	II	III
Eigenvalue	1.18	0.43	0.34
Chi-square test for significance of discriminant function	108	49	22
Degrees of freedom	30	18	8
Significance	***	***	0.004
Percent of discriminating information	61	22	17
Variable	Rotated Standardized Discriminant Function Coefficients		
Deciduous cover above 8m (DEC)	0.984	-0.187	0.107
Aspen density (ASPEN)	-0.442	-0.229	0.228
Shrub cover 1-2m (SHRUBS)	0.334	-1.548	-0.293
Shrub cover 2-4m (SHRUBM)	0.282	1.208	0.338
Number of plots without trees (MISSTREE)	0.268	0.945	0
Bunch grass cover (BUNCH)	0.261	-0.918	0.105
Shrub cover 0-1m (SHRUBL)	-0.203	0.717	-0.395
Conifer cover 1-2m (CONS)	0.089	0.321	1.030
Conifer cover above 8m (CON)	0.422	0.173	0.681
Conifer cover 2-4m (CONM)	-0.160	-0.009	-0.435

*** = $P < .001$

cover in the 4-8 m height class. The screech owl loaded positive and very high on this variate; the boreal owl had a negative and moderate loading (Fig. 4). Canonical variate II represents a gradient of shrub cover and habitat patchiness (indicated by high correlation with MISSTREE). Habitats with 1-2 m shrub cover, bunchgrass cover, and trees in most plots represented the negative end of the gradient; more open habitat with 0-1 m and 2-4 m shrub cover represented the positive end. The great-horned owl loaded highly on this variate, reflecting its use of open shrubby habitats. Coniferous cover at various heights was represented by the third canonical variate. High loading of the boreal owl on this variate indicates use of coniferous stands having well-developed low and high canopy but lacking a mid-canopy layer. Saw-whet owls loaded moderately on all three variates but show a tendency toward non-deciduous forest stands with a well-developed mid canopy layer and shrubs in the 1-2 m height class.

The degree of overlap between species on the three most discriminating microhabitat variables can be visualized from Figure 3. Saw-whet, screech, and boreal owl microhabitat structures overlap little. By plotting each observation in discriminant space, species' variability in each habitat dimension is shown. The saw-whet owl shows little variability on axes I and III indicating a narrow range of habitat selection for non-deciduous stands (variate I) and even aged, single layered conifer habitats (variate III). Boreal and

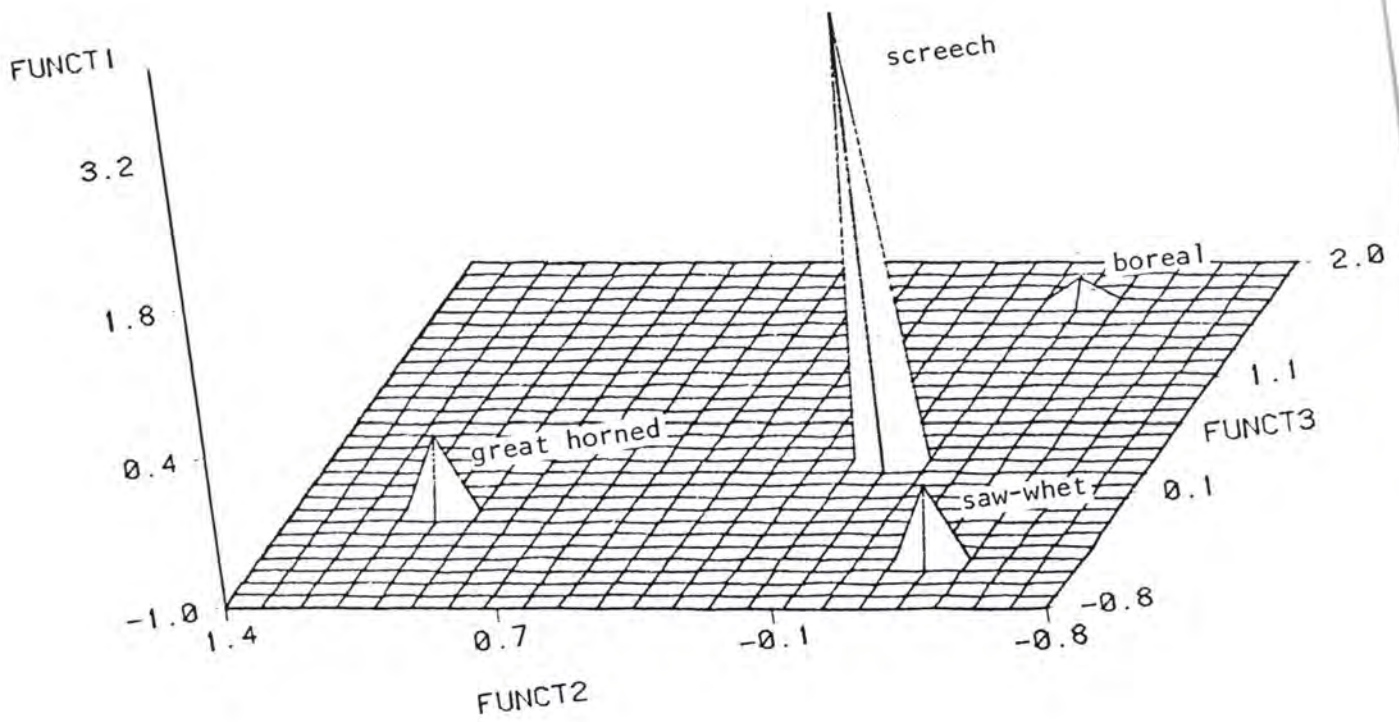


Fig. 4. Species centroids for four owls on three canonical discriminant axes representing microhabitat niche space. See text and Figure 5 for description of each canonical discriminant axis.

screech owls also show less variability on two dimensions and substantial dispersion in a third (boreal owls on variates I and II, screech owls II and III). The dispersion of values for both great-horned and pygmy owls indicates less specific microhabitat selection for the variables measured.

A more direct measure of species' overlap and the power of the discriminating variables is to determine the accuracy of the canonical variates in predicting group membership. The proportion of correct classifications relates to the power of the discriminating variables, and the pattern of classification reflects the species' overlap in microhabitat niche (Table 10). Over two thirds of the observations were correctly classified. All misclassified boreal owls were classified as saw-whet owl, the boreal owl's congener. The smaller saw-whet owl was rarely misclassified as a boreal owl. No owls were misclassified as screech owl although saw-whet and great-horned owls sometimes occupied territories adjacent to screech owls along Big Creek.

The significance of segregation along each canonical axis, was determined by analysis of 95 percent confidence intervals for species' centroids (Fig. 5). The screech owl differed from all others in the amount of deciduous cover (axis I). Segregation of great-horned, from saw-whet, boreal, and screech owls is evident on axis II. Boreal owl habitats differed from great-horned and saw-whet owl habitats on axis III. Significant segregation ($p < 0.05$) on at least one axis occurred between all species' pairs except pygmy/boreal,

Table 10. Classification matrix for four owl species across both study sites.

Actual group	N	Predicted group membership			
		SW	SC	BO	GH
Saw-whet	45	73% (33)	0% (0)	7% (3)	20% (9)
Screech	8	25% (2)	63% (5)	0% (0)	12% (1)
Boreal	8	25% (2)	0% (0)	75% (6)	0% (0)
Great horned	23	17% (4)	0% (0)	17% (4)	66% (15)

Percentage of individuals of all species correctly classified = 70.2%

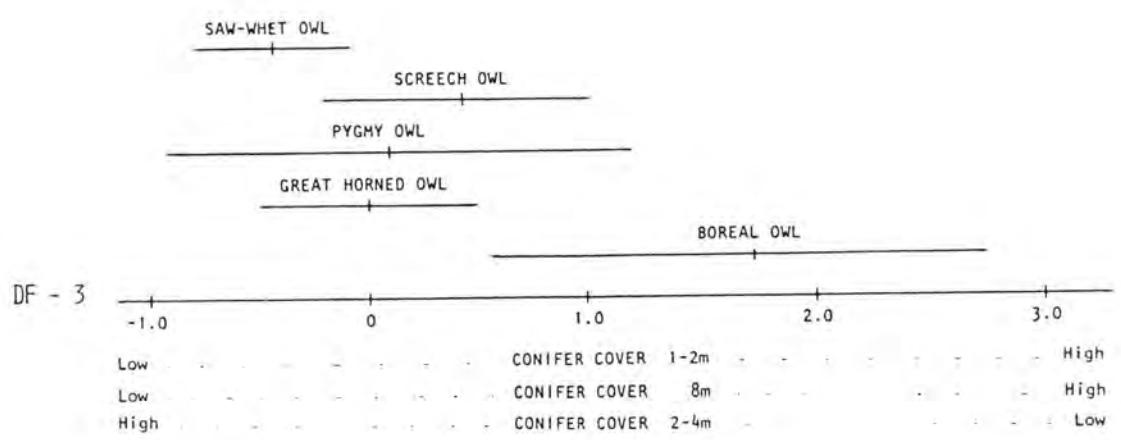
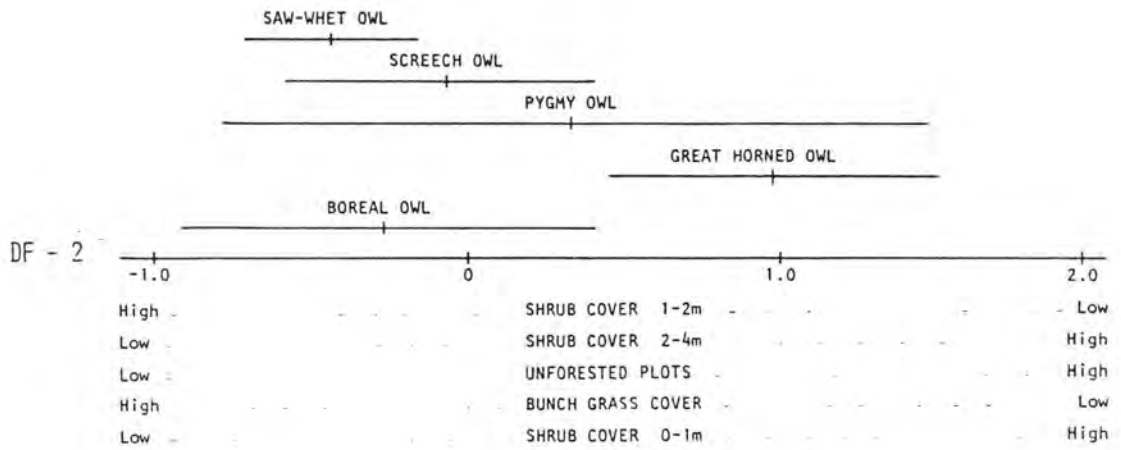
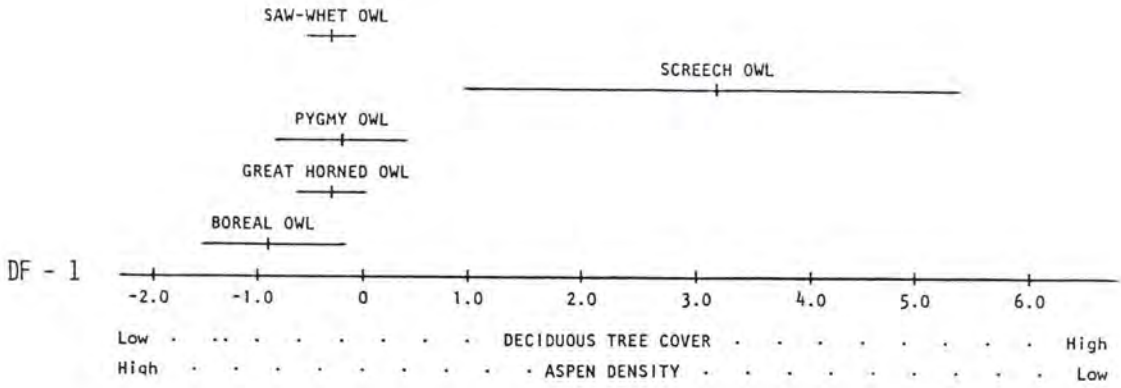


Fig. 5. Mean owl positions and 95% confidence intervals on three independent canonical discriminant axes for combined analysis.

pygmy/great-horned, and pygmy/saw-whet.

Substantial differences between vegetations at Chamberlain and Taylor provide a means for comparing the niche dimensions most responsible for species' habitat segregation. Patterns in habitat segregation may be recognized through examination of separate analyses of habitat segregation at each study site and the previous analysis of all observations. Appendix 1 and 2 contain summary information from separate stepwise canonical discriminant analysis for Chamberlain and Taylor, respectively.

The canonical variates which most effectively separate the owl habitats at each study site are related to those of the combined analysis. The patterns of classification also support the earlier findings on habitat preference. Two canonical variates derived for the Taylor site data separate screech owl habitat from that of saw-whet and great-horned owls. Although three species use habitats along Big Creek, screech owls are strictly confined to the riparian zone. The screech owl uses a wide range of deciduous habitats - probably most habitats along Big Creek (Fig. 5). A portion of these deciduous habitats are also used by other species. The canonical analysis chose variables (DEC, SHRUBM, SHRUBS) which emphasize the minor differences in habitats used by species along the riparian area. Possibly this indicates the area of greatest diffuse competition.

As in the overall canonical discriminant analysis, canonical variate I relates most to deciduous cover at 4-8

meters. Variate II defines a gradient from patchy (MISSTREE) habitat with 2-4 m shrub cover and tall conifer cover to more homogenous cover including 1-2 m shrubs. The positive end of variate II corresponds to streamside habitats with 9-18" DBH Douglas fir and an understory of birch, alder, and hawthorn. These habitats occur along Big Creek and are often used by screech owls. Species means on the canonical variates reinforce conclusions drawn from the combined analysis. The saw-whet owl loads highly but negatively on axis II, suggesting selection of a uniformly timbered habitat (MISSTREE) with 1-2 m shrubs (Appendix 1). That the great horned owl loads oppositely on function II suggests preference for more patchy cover.

The pattern of classification by discriminant analysis for Taylor (Appendix 1) again indicates that in the microhabitat niche, screech owls overlap the most with other owls. As in the overall analysis, no owls were missclassified as screech owl. Screech owl habitat, in contrast, was often misclassified as another species'.

Whereas the canonical analysis at Taylor concentrates on separating one species (screech owl) from the other two, at Chamberlain the microhabitat of three species is more distinct. At Taylor one habitat (the riparian zone) is used by three species but at Chamberlain no one habitat seems to receive such concentrated use. For the Chamberlain analysis, variate I is correlated with mid-canopy conifer cover and non-grass ground

cover. High values on variate II describe habitat which has little horizontal variation in vegetation cover (-HDIV), grass ground cover, and canopy cover above 8 meters high. The distribution of species' means on the canonical axis (Appendix 2) show that saw-whet and great-horned owls are widely divergent on both axes. Boreal owl differs from saw-whet on axis I and great-horned on axis II. As in both previous analyses, saw-whet owl habitat is relatively homogeneous (-HDIV on axis II). Classification results (Appendix 2) indicate that the two canonical variates are highly effective in distinguishing species' habitat.

Examination of means and coefficients of variation (C.V.) of habitat variables may reveal which variables are important in a species' habitat selection (Table 11). Where one species' C.V. is markedly smaller than the others, course grain perception is implied (Vandermeer 1972), and the species is selecting a narrow range of the available habitat (highlighted, Table 11). Some variables have low C.V. across all species. These variables may be invariant throughout the habitats sampled or characteristics narrowly selected by all species. Screech owls chose significantly greater shrub cover values in the 1 to 8 m height class and the low C.V. indicates that this behavior occurred consistently. Boreal owls chose sites with greater cover high in the canopy (4 meters and higher), more abundant large (> 60 cm dbh) trees, and less non-grass ground cover than other owls.

Table 11. Means and coefficients of variation for the important microhabitat variables at each study site. Values are calculated from transformed data as outlined under methods. Mnemonics for the habitat variables are from Table 2; PY=Pygmy owl, SW=Saw-whet owl, BO=Boreal owl, SC=Screech owl, and GH=Great horned owl.

Variable	Taylor				Chamberlain			
	PY	SW	SC	GH	PY	SW	BO	GH
SHRUBL	0.33 0.61	0.40 0.68	0.48 0.33	0.49 0.56	0.09 0.21	0.15 0.40	0.12 0.83	0.23 0.72
SHRUBS	0.19 0.92	0.19 0.84	*0.41 0.38	0.25 0.86	0.0 0.0	0.05 0.53	0.04 0.31	0.05 0.58
SHRUBM	0.12 1.77	0.09 1.06	*0.30 0.45	0.19 1.15				
SHRUBT	0.09 1.40	0.05 0.90	*0.15 0.84	0.08 1.26				
CONL	0.05 0.75	0.05 0.65	0.04 0.27	0.04 0.43	0.16 0.91	0.11 0.54	0.14 0.62	0.11 0.68
CONS	0.11 0.74	0.09 0.64	0.08 0.53	0.09 0.62	0.31 0.34	0.14 0.53	0.22 0.58	0.19 0.64
CONM	0.26 0.61	0.23 0.57	0.12 0.45	0.21 0.64	0.55 0.57	0.24 0.44	0.34 0.53	0.31 0.30
CONT	0.30 0.35	0.36 0.40	0.23 0.49	0.34 0.46	0.67 0.99	0.35 0.40	*0.52 0.33	0.40 0.45
CON	0.37 0.72	0.49 0.45	0.56 0.44	0.52 0.42	0.58 0.62	0.50 0.41	*0.58 0.34	0.41 0.61
DECT	0.06 1.06	0.10 0.82	0.49 0.75	0.16 1.18				
DEC	0.05 0.87	0.04 0.37	*0.32 1.06	0.04 0.11				
HDIV	0.38 0.53	0.36 0.39	0.47 0.44	0.41 0.38	0.43 0.49	*0.23 0.36	0.31 0.35	0.38 0.29
VERTHT	2.13 0.11	2.07 0.09	2.17 0.02	2.11 0.06	2.10 0.04	1.98 0.11	2.00 0.12	2.08 0.06
BUNCH	0.18 0.77	0.16 0.78	0.10 0.97	0.11 0.71	0.04 0.14	0.08 0.85	0.10 0.67	0.05 0.59
TURF	0.17 0.69	0.19 0.90	0.16 1.04	0.18 0.81	0.25 0.22	0.40 0.56	0.28 0.39	0.36 0.30
FORB	0.37 0.37	0.30 0.44	0.32 0.28	0.36 0.52	0.20 0.48	0.55 0.22	0.29 0.28	0.45 0.18
MALL	0.53 0.29	0.48 0.37	0.43 0.40	0.50 0.47	0.36 0.30	*0.81 0.31	0.49 0.17	0.65 0.18
MISSTREE	9.30 0.64	5.38 0.72	6.38 0.71	6.71 0.57	1.00 1.41	1.13 1.87	1.50 1.33	4.00 1.37
MTH	30.7 0.86	32.1 0.73	40.7 0.61	11.0 1.98		41.7 0.50	29.9 0.96	12.2 1.61
SEED	0.46 1.30	0.28 1.08	*0.49 0.53	0.42 1.20	1.30 0.32	1.15 0.47	1.08 0.61	1.19 0.67
SAP	0.58 0.81	0.37 0.87	*0.49 0.74	0.38 1.15	1.23 0.18	1.51 0.58	1.11 0.60	1.10 0.72
POLE	0.50 0.84	0.44 0.69	0.40 0.65	0.37 0.71	0.73 0.09	1.12 0.49	*0.72 0.64	1.05 0.62
MATURE	0.34 1.15	0.52 0.69	0.58 0.67	0.54 0.64	0.32 0.20	*0.60 0.68	0.45 0.92	0.44 0.84
OLD	0.59 0.55	0.59 0.47	0.56 0.53	0.67 0.44	0.36 0.74	0.13 2.06	*0.34 0.92	0.13 1.55
ASPEN						0.01 3.14	0.01 2.93	0.01 3.86
Sample size	6	37	8	14	2	8	8	9

At both Chamberlain and Taylor, the low C.V. for mid, high, and upper conifer canopy cover was consistent across all species. Although C.V. values were consistent the means for both mid (2-4m) and high (4-8m) conifer cover were significantly different ($p=0.07$) across all species at Taylor indicating that species used forests of different foliage density. At both study sites, pairwise differences between species appear in both mid canopy (CONM) and high canopy (CONT) cover.

Saw-whet owl orientation to mid, high, and upper conifer cover is strikingly consistent between the two study sites. This provides evidence that the saw-whet owl is not simply utilizing the only available vegetation structure; rather it is selecting coniferous stands with particular structural characteristics.

R - Factor Analysis

"Factor analysis is a strategy for reducing large correlated categorical data into a smaller number of uncorrelated factors" (Aspey and Blankenship 1977) in order to determine the structure among the multiple variables. Bhattacharyya (1981) describes the statistical technique and Smith (1977), Connor and Adkisson (1977), and Whitmore (1977) developed its application for habitat analysis. Rather than identifying those variables which maximize species segregation, factor analysis identifies factors which describe the

vegetation structure characteristics most important in the sample. An ordination may be developed by plotting the factor scores of each observation on the factor axes. In such a plot, grouping of observations by species indicates relative position of species' niches and the degree of species' segregation in the factor space.

Four meaningful factors derived for Chamberlain accounted for over 81 percent of the total variance and had eigenvalues greater than unity (Table 12). The fifth factor, may be ecologically meaningful but adds little to the overall interpretation. The first factor represents a gradient from conifer cover to non-timbered, low shrub habitat; i.e., from forested slopes to sagebrush openings on southwest exposures. Factor two is related to conifer stem density and represents a gradient from sapling and pole timber to large-diameter timber. At Chamberlain this corresponds to differences between the extensive lodgepole pine stands and the mature mixed conifer stands confined to the dryer exposures. High values on the third factor represent conifer cover in the 2-4m height class. Density of mature (23 to 38 cm dbh) conifer is represented by factor four.

Conifer cover and tree density variables are confined to separate factors; this implies independence between these habitat characteristics. Furthermore, conifer cover near the ground appears to be relatively independent from the upper canopy as indicated by factors I and II.

Table 12. Varimax rotated factor pattern for microhabitat variables at Chamberlain. Zero factor loading was 0.45 throughout and loadings greater than 0.55 were used to interpret factors.

Variable	Factor			
	I	II	III	IV
Number of plots without trees (MISSTREE)	-0.651			
Shrub cover 0-1m (SHRUBL)	-0.707			
Conifer cover above 8m (CON)	0.858			
Conifer cover 4-8m (CONT)	0.512			
Density 3-6" dbh trees (SAP)	0.501	0.688		
Density 6-9" dbh trees (POLE)		0.844		
Density 9-15" dbh trees (MATURE)				0.684
Density large dbh trees (OLD)		-0.841		
Density aspen (ASPEN)				0.823
Ground cover (MALL)			-0.433	
Conifer cover 1-2m (CONS)			0.957	
Conifer cover 2-4m (CONM)			0.849	
Eigenvalue	4.03	2.81	1.26	1.10
Percent of variance explained	39.5	27.6	12.4	10.8
Cumulative percent of variance	39.5	67.1	79.5	90.3

Habitat of great-horned and saw-whet owls is similar with respect to four factors (Fig. 6). These species occupy essentially the same area on all four axes. Microhabitat used by the boreal owl, however, is different from the other species by a combination of Factors I and II. It selects stands with a well-developed upper canopy and trees of a large diameter class.

Three of five factors derived for Taylor are essentially the same as those calculated for Chamberlain (Table 13). The first factor represents deciduous cover of tall shrubs and cottonwoods. These structural features are not found in the Chamberlain vegetation. Low and mid canopy conifer cover form Factor II (Factor III at Chamberlain). Upper canopy cover and the frequency of plots lacking trees (MISSTREE) are again correlated. These formed Factor III (Factor I at Chamberlain). Factor IV corresponds to the density of mid-diameter trees (Factor II at Chamberlain).

All owls except screech owls are narrowly distributed near zero on Factor I (Fig. 7). The screech owl alone exploits habitats with a broad range of deciduous cover. Saw-whet and great-horned owls overlap extensively on all four factors.

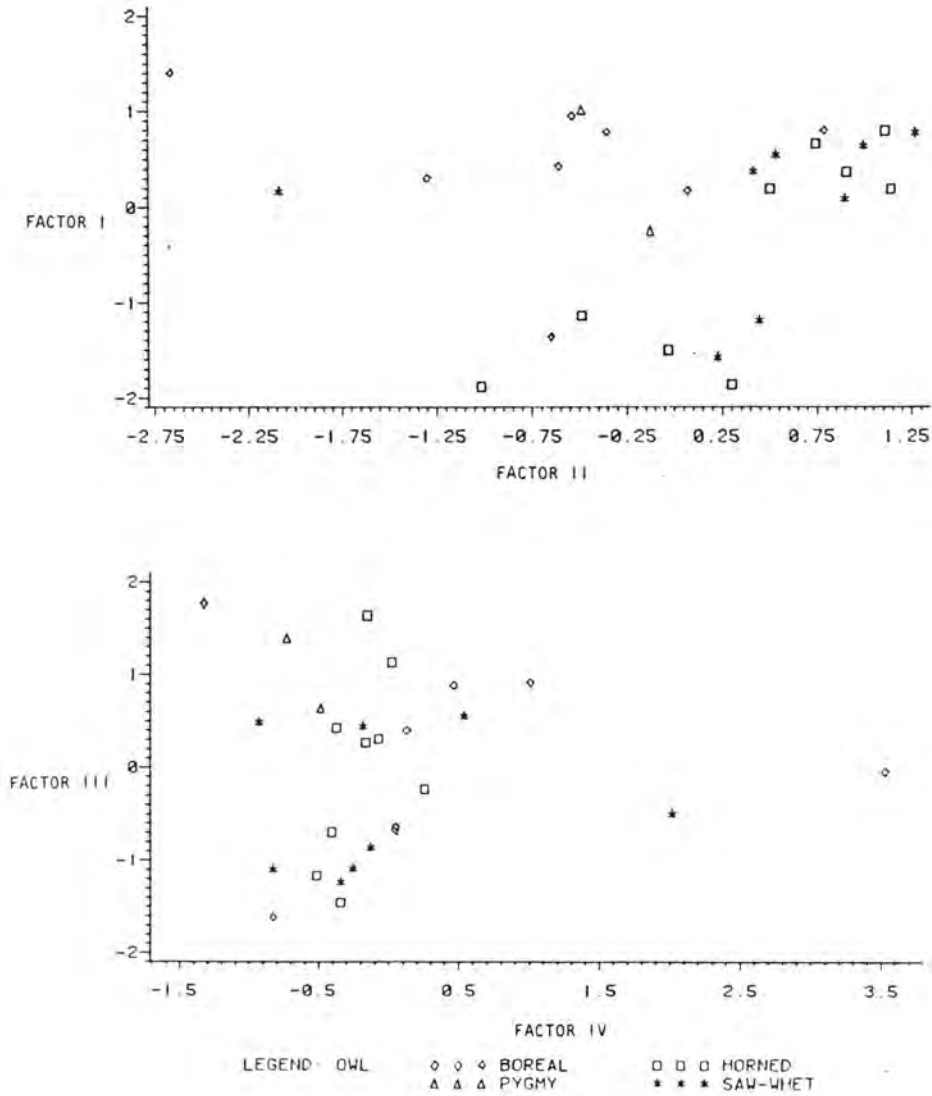


Fig. 6. Factor loadings of four owl species on four, varimax rotated factors extracted by R-factor analysis. Axes represent microhabitat characteristics important in owl use areas at Chamberlain. Factor I = Canopy cover and tree dispersion; Factor II = Conifer density and diameter; Factor III = Mid canopy conifer cover; Factor IV = Mature conifer density.

Table 13. Varimax rotated factor pattern for microhabitat variables at Taylor. Zero factor loading was 0.45 throughout and loadings greater than 0.55 were used to interpret factors.

Variable	Factor			
	I	II	III	IV
Deciduous cover above 8m (DEC)	0.703			
Deciduous cover 4-8m (SHRUBT)	0.893			
Shrub cover 2-4m (SHRUBM)	0.707			
Shrub cover 1-2m (SHRUBS)	0.508			
Shrub cover 0-1m (SHRUBL)				
Conifer cover 1-2m (CONS)		0.713		
Conifer cover 2-4m (CONM)		0.923		
Conifer cover 4-8m (CONT)		0.661		
Number of plots without trees (MISSTREE)			-0.823	
Conifer cover above 8m (CON)			0.838	
Ground cover (MALL)				
Density 3-6" dbh trees (SAP)				0.488
Density 6-9" dbh trees (POLE)				0.889
Density 9-15" dbh trees (MATURE)				0.573
Density large dbh trees (OLD)				
Eigenvalue	4.18	3.00	1.53	1.12
Percent of variance explained	37.5	26.9	13.7	10.0
Cumulative percent of variance	37.5	64.4	78.2	88.2

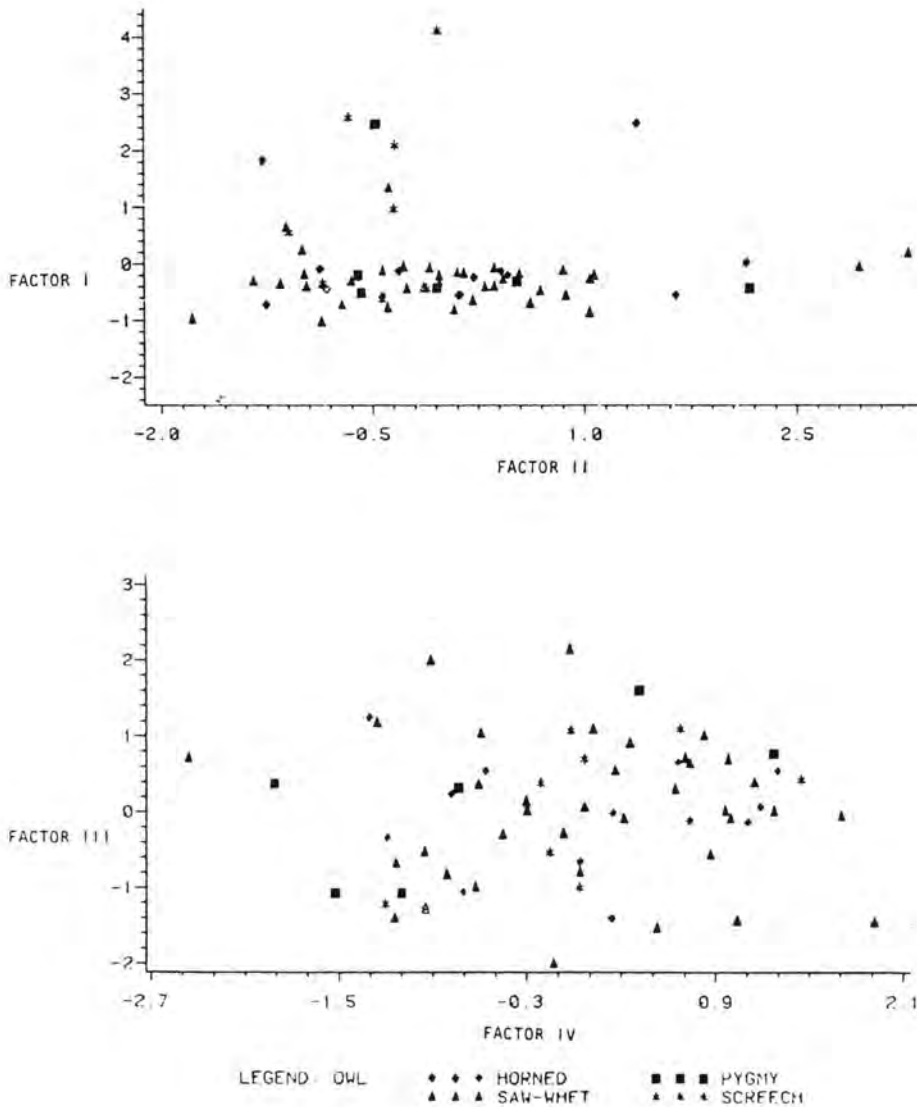


Fig. 7. Factor loadings of four owl species on four, varimax rotated factors extracted by R-factor analysis. Axes represent microhabitat characteristics important in owl use areas at Taylor. Factor I = Deciduous and tall shrub cover; Factor II = Low and mid canopy conifer cover; Factor III = Upper canopy cover and tree dispersion; Factor IV = Density of pole size trees.

Temporal Niche

Circadian Activity: Radio-tagged boreal, saw-whet, and screech owls all began foraging each evening within 45 minutes of sunset. They retired to the day roost within 30 minutes of sunrise (Table 14). Sunrise/sunset determinations from the 1981 Astronomical Almanac are based on azimuth $90^{\circ} 50'$ from the suns' zenith. Mountainous terrain made actual sunrise-sunset times later and earlier respectively. In Table 14 those occasions indicated as 'Left roost' refer to instances when I located a roosting owl in late afternoon and observed the owl until it left the roost. [All three species, on at least one occasion ejected a pellet immediately prior to leaving the roost.] Those occasions indicated 'Foraging' refer to occasions when the roosting owl was not located but an erratic signal indicated the owl was moving at least by the time noted. The cessation of foraging in the morning was determined by the consistent radio signal from one location. The circadian activity of the boreal owl was monitored during its nesting period (Fig. 8).

No data was obtained for the activity period of pygmy and great-horned owls and few other investigations have specifically measured the circadian rhythm of forest owls. In northern Idaho, Frounfelker (1977) observed radio-tagged great-horned owls beginning activity at sunset. In Colorado

Table 14. Summary of data on active period for three species of owls. Observations were made of radio-tagged owls which were observed leaving their roost or determined to be foraging based on characteristics of the radio signal.

Species	Activity	Time	Sunrise/Sunset	Difference
Boreal owl	Foraging	1810	1735	45
	Roosting	0745	1738	7
	Foraging	1720	1740	-20
	Roosting	0630	0702	32
	Left roost	1919	1921	-2
	Capture - foraging	1940	1915	25
Saw-whet owl	Roosting	1620	1628	8
	Foraging	1905	1905	0
	Left roost	1943	1921	22
	Left roost	1955	2042	13
Screech owl	Left roost	1815	1758	17
	Roosting	0730	0745	15
	Left roost	2115	2110	5
	Left roost	2103	2115	-12
	Foraging	2145	2118	27
	Left roost	2132	2131	1
	Foraging	2127	2132	-5
	Foraging	2140	2139	1

Note: Difference indicates number of minutes into the dark. A negative value in the morning indicates activity after sunrise.

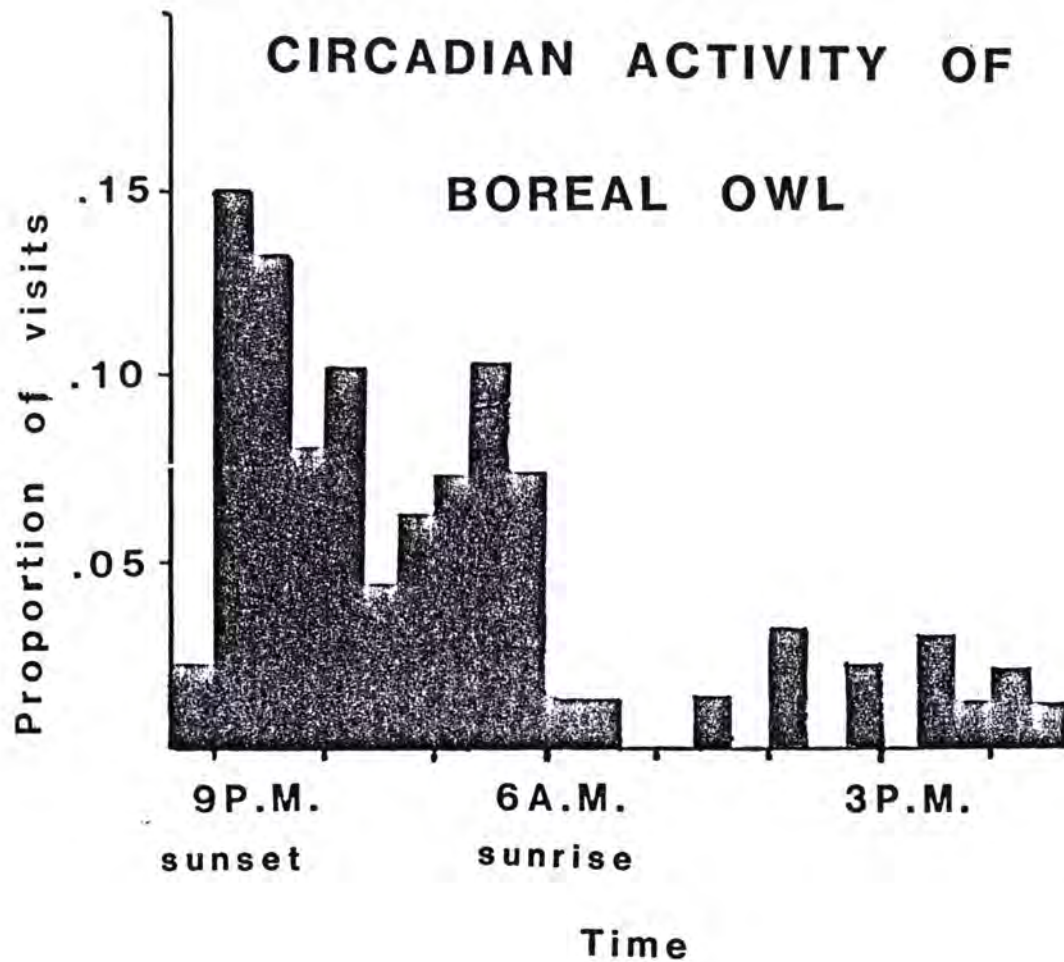


Fig. 8. Circadian activity of boreal owl recorded at a nest site in the River of No Return Wilderness, Idaho, over a nine day period.

great-horned owls began hunting before complete darkness; departure averaging 20 minutes after sunset (Marti 1974). Lacking sound information, the pygmy owl is characterized as hunting mostly during daylight hours (Sprunt 1955, Eckert and Karalus 1974).

Studies by Graber (1962) on saw-whet owl and Klaus et al. (1975) on the boreal owl show both species exhibit a biphasic circadian rhythm with activity peaks at nightfall and again just before dawn. Norberg (1964) found boreal owls first visiting their nest 40-60 minutes following sunset. These three studies support the weak trends shown in Table 14 of activity beginning at dark and ending at dawn for boreal and saw-whet owls. Van Camp and Henny (1975) feel screech owls are highly nocturnal, and Allen (1924) noted prey deliveries to a nest throughout the night, again supporting my data.

Annual Activity: I found one active boreal owl nest and one family group each of the saw-whet and screech owl. Information on incubation and fledging periods from Kuhk (1949) for boreal owls, Van Camp and Henny (1975) and Bent (1961), for screech owl and Bent (1961) for saw-whet owl were used to estimate the laying and hatching dates for the three nests (Table 15). Egg dates which Eckert and Karalus (1974) cited as most common are listed in Table 16.

Chapter 3 discusses owl movements and home range use. All species except the flammulated owl, were located in the study

area during winter and appeared to establish breeding territories in the areas used during winter.

Table 15. Estimates of laying, hatching, and fledging dates from observations of one boreal owl nest and a family group each of screech and saw-whet owl. Estimates are back-dated from observations using information from Bent (1961).

Species	Estimated laying date	Estimated hatching date	Estimated fledging date
Boreal	27-29 April	24-26 May	23-25 June
Screech	13-19 April	15-21 May	11-15 June
Saw-whet	20-26 April	16-22 May	13-19 June

Table 16. The most common period when eggs are recorded in nests of five owl species. From Eckert and Karalus (1974).

Species	Eggs in nest
Flammulated owl	4 June - 21 June
Pygmy owl	8 May - 24 June
Saw-whet owl	6 April - 2 May
Boreal owl	16 April - 20 May
Screech owl	26 March - 7 May
Great horned owl	20 February - 25 March

Food Niche

Fifteen prey species were identified from pellets found beneath roosts and in nest cavities of four owl species (Table 17). Radio-tagged saw-whet, screech, and boreal owls provided the majority of food habits material. Locating pellets of great-horned and pygmy owls was extremely difficult without radio-marked individuals.

A slightly significant ($p = 0.046$) difference in the size and life form of prey chosen by the three most similar size owl species was demonstrated by a chi-square test (Table 18). A high proportion of very small mammals (2-15g) occurred in the saw-whet owl diet, whereas low numbers of very small mammals were taken by boreal owls. This difference contributed most to the significant test. Small mice dominated the diets of all three species.

In other areas saw-whet owls consume mainly Peromyscus (Spurr 1952) with an increase in frequency of birds in spring (Graber 1962); boreal owls concentrate on Microtus and Clethrionomys (Norberg 1964, Sulkava and Sulkava 1971, Bondrup-Nielsen 1978) but also take birds when small mammals are scarce (Klaus et al. 1975); great horned owls kill a variety of mammals, birds, amphibians, and reptiles ranging in size from snowshoe hares (Lepus americanus) to mice (Earhart and Johnson 1970); and pygmy owls take small mammals, birds, and insects in almost equal proportions (Earhart and Johnson

Table 17. Prey of four owls in the River of No Return Wilderness, Idaho. Highlighted weights are from Marti (1976), otherwise from author's unpublished data and from field guides.

Prey	Weight (grams)	Owl Species			
		SW	BO	SC	GH
Insect	0.5	2	9	1	
Mammal					
Sorex spp.	8	4	1	2	
Sorex vagrans	8	1			
Peromyscus maniculatus	21 *	8	7	4	1
Clethrionomys gapperi	25 *	1	31		
Phenacomys intermedius	30	1	3		
Microtus longicaudus	40	2			
Microtus spp.	43 *		1		
Microtus montanus	47 *		1		
Glaucomys sabrinus (juv.)	80		1		
Thomomys talpoides	104		2		
Neotoma cinerea	300			1	2
Sylvilagus nuttalli	800		1		1
Unknown mammal		7	11	7	1
Birds					
Unknown bird		1	8	1	
Bubo virginianus					1

Table 18. Comparison of prey type and size class of three owls in the River of No Return Wilderness, Idaho. Each cell displays prey frequency .
cell chi-square

Prey type - size class		Owl Species		
		SAW-WHET	BOREAL	SCREECH
Insect		2 0.3	10 0.3	1 0.3
Mammal	2-15g	7 4.6	3 3.9	4 2.4
	16-35g	15 0.1	49 0.3	7 0.7
	36-60g	2 0.3	2 0.9	2 1.8
	> 60g	0 1.1	4 0.2	1 0.2
Bird		1 0.7	8 0.4	1 0.1

Chi-Square = 18.6

DF = 10

P = 0.046

1970). The food habits of western screech owls are not well documented and prey of this species varies geographically such that generalizations would be more tenuous than for the preceding species.

DISCUSSION

Most ecological studies of birds of prey focus on the feeding niche and/or the role that competition for food plays in regulating the abundance and distribution of species (Clark et al. 1978). These studies have shown that prey availability may influence owl populations. In European boreal owls, the influence of limited prey on population densities and movements has been demonstrated by Mysterud (1970) and Lundberg (1979). Southern (1970) showed that food ultimately limits populations of tawny owls by affecting territory size and breeding success. Southern and Lowe (1968) emphasized the role of habitat in determining vulnerability of prey and success of tawny owl pairs. Although Lack (1946), Herrera and Hiraldo (1976), and Marti (1974) sought to characterize the food niche of owls in general, in Europe, and in northern Colorado, respectively, they alluded to the opportunity for these birds to segregate on complementary niche dimensions in order to relieve substantial overlap in diet. Marti (1974) showed that four owl species

specialized on different "groups and sizes of prey." Long-eared, barn and great-horned owls, however, consumed 88.8%, 54.1%, and 64.1% respectively of their prey from two size classes (20-30 and 30-50 g). In Scandanavia, diets of seven owl species are over 50% Microtinae (Herrara and Heraldo 1976). Overlap in prey consumption by owls, then, is substantial. My study sought to identify which niche dimensions are most significant in segregating the seven forest owls occurring in the RNRW.

Niche Pattern

My observations indicate that segregational differences within the forest owl guild encompass all four major niche dimensions, macrohabitat, microhabitat, time, and food. I view resource partitioning as a hierarchial process (Fig. 9). Ecological isolation high in the hierarchy can permit complete overlap at lower levels. Natural selection will encourage species' differences at some level; however, the degree of segregation necessary to allow coexistence is not known. Studies of resource partitioning begin by looking for gross differences in species niches. If there is complete segregation on a large scale then there is no reason to search for finer scale segregation. Differences in macrohabitat occur at the upper level of the hierarchy and often are most easily recognized. Non-overlapping geographic or altitudinal

Resource Partitioning

Initial
level of
segregation

MACROHABITAT – Geographic

Black-backed
Three-toed Woodpecker
Coniferous boreal forest of N.A.

Acorn Woodpecker
Oak woodlands of Southwestern N.A.

MICROHABITAT – Foraging Habitat

Northern Three-toed
Woodpecker
*Forages on thin-barked
Lodgepole pine*

Black-backed
Three-toed Woodpecker
*Forages on thick-barked
Ponderosa pine*

TEMPORAL – Daily or Seasonal Activity

Not recognized among these woodpeckers

Ultimate
level of
segregation

FOOD (or special requirements)

Williamson's Sapsucker
Feeds on sap from sapwells

Black-backed
Three-toed Woodpecker
Excavates, scales, pecks, and greans for insects

Fig. 9. Hierarchy of resource partitioning. Differences among species in resource utilization are most easily recognized high in the hierarchy and studies of resource segregation should concentrate here first.

distributions relieve competition at all lower levels and may be a consequence of extreme similarity in other resource dimensions (MacArthur 1972). Microhabitat segregation, the second level, is followed by temporal differences. Food niche differences represent an even finer level of resource subdivision. In any guild there may be additional limiting resources, such as nest sites for cavity nesting birds, which may require segregation in utilization. Coexistence, however, requires some limiting dissimilarity within the habitat - food hierarchy. Niche differences at one level may be a consequence of ecological divergence at another level. For instance, nonoverlapping food habits may be a result of segregation at the microhabitat level because different prey species are available in different habitats.

Macrohabitat niche segregation is most important for the screech owl. Boreal and screech owls are similar in size (160 g and 215 g respectively), but differ in macrohabitat through nonoverlapping elevational distributions. Both species concentrate on small mammal prey but will capture birds and insects while feeding young. These similar habits indicate that the potential for competition may be high. In addition, both are cavity nesters and presumably would require similar size cavities.

With the exception of the saw-whet owl at Chamberlain Basin, owl territories contain mixtures of vegetation types different from the mixture available in the study area. The

owls appear to be choosing breeding territories in a nonrandom fashion but macrohabitat differences among sympatric owls were only significant at Taylor (see Tables 5,6). Habitats used by screech, great-horned, and saw-whet owls do overlap however, pressing the issue of limiting similarity. Being confined to the valley bottom habitats along Big Creek, screech owl macrohabitat selection may effectively separate its niche from other members of the guild. Does the screech owls' exclusive use of the densest deciduous bottom habitat sufficiently segregate it from both great-horned and saw-whet owls to avoid competition for food?

Overlap in habitat used by screech owls and either saw-whet or great horned owls is further shown by misclassification of screech owl microhabitat. However, neither saw-whet nor great-horned microhabitat was misclassified as screech owl habitat. This indicated that in spite of overlaps in distribution, microhabitat differences do exist among these species but their habitat use along riparian areas is similar.

Several other species pairs separated most clearly on the basis of microhabitat vegetation characteristics (Fig. 10). Saw-whet and boreal owls differed mainly in the structure of coniferous trees within their habitats. Saw-whet owls in comparison with boreal owls, chose stands of smaller trees having fewer large openings, greater overall canopy closure, and greater canopy cover in the mid canopy. Whereas saw-whet

	GH	PY	SC	SW		
BOREAL OWL	/	/	/	/		
GREAT HORNED OWL			—		symbol	discriminant function
PYGMY OWL			—		—	1
SCREECH OWL				—		2
					/	3

Fig. 10. Results of Bonferoni multiple comparison of mean discriminant scores among all possible pairs of species on each function. Symbols denote significant differences (see text).

owls hunt within relatively dense coniferous timber, a radio-tagged boreal owl hunted an open stand of oldgrowth timber and along forest-shrubfield edges.

The geographic distributions of saw-whet and great-horned owls observed in the RNRW are almost identical. Both were located at all three study camps, and individuals sang within 0.4 km of one another. Although macrohabitats, were similar, significant differences occurred in such microhabitat characteristics as shrub cover and number of forest openings. Boreal and great-horned owls likewise showed only moderate overlap in their selection of microhabitat features.

Pygmy owl habitat associations were not clear from available data. The species occurred at both Chamberlain and Taylor and seemed to be associated with open, large diameter conifer stands. Overlap in microhabitat between the pygmy owl and other species was substantial.

MacArthur (1958), Cody (1974), and Pianka (1978) suggested that differences in time of activity and breeding period may be dimensions for niche segregation. To reduce competition for food through temporal segregation, the predators' prey populations must be independently renewing in terms of time. Or, the actions of a predator during one period must not substantially affect prey of the other predator during its active period. My data suggest that saw-whet, boreal, and screech owls overlap substantially in both daily foraging period and breeding season. Great-horned owls also are

crepuscular to nocturnal hunters.

Pygmy owls, however, are diurnal to crepuscular (Bent 1961, Eckert and Karalus 1974) and consume a wide range of prey (Brooks 1930). This is unusual in that smaller predators usually tend to consume a narrow range of prey sizes. Daytime hunting by a temperate forest owl may be viewed as a specialist strategy to avoid competition with nocturnal predators of small vertebrates. The eye and ear structure of pygmy owls appear as fit for nocturnal foraging as that of other owls in the community.

The only flammulated owl located (they may be much more common than indicated by the data) sang on four successive nights no more than 30 m from a boreal owl nest. Typical habitat of this strictly nocturnal owl (Hayward in review) is open, mature conifer stands similar to those used by boreal owls at Chamberlain (Marshall 1939). Flammulated owls are the only strictly migratory owls in the area. They do not begin breeding until June, after other owls have young in the nest or fledged. Probably more important for niche separation, flammulated owls are strictly insectivorous, feeding mainly on nocturnal moths (Johnson and Russell 1962, Marshall 1939). Resource partitioning for this species appears to occur at the level of the food niche.

The question of limiting similarity (MacArthur (1972) cannot be resolved by my limited data. Overlap in prey size class of sympatric saw-whet/boreal and saw-whet/screech owl

pairs did appear substantial, however. Whether sympatric great-horned, boreal, saw-whet and pygmy owls consume similar prey can not be answered. However, boreal/pygmy and saw-whet/pygmy owl pairs likely overlap substantially in prey size class consumed. Diets of great-horned owls may not overlap substantially with those of the smaller forest owls.

Foraging behavior and morphology of forest owls may help explain the mechanisms of prey and habitat segregation among species. As Hespeneheide (1973, 1975) argues, competing species should adjust niche widths through character displacement by restricting or expanding habitat preference or foraging behavior, rather than diet. Differences in morphology related to foraging (searching, method of pursuit) rather than prey capture (subduing prey) should be most indicative of important niche differences between competing species. In owls, differences in the structure of wings, eyes, and ears rather than feet may reveal niche differences among close competitors.

Differences in the size and degree of asymmetry in owls' ears may relate to their foraging behavior as could variation among species' visual capabilities. Few data are available on vision or hearing for the small owls found in the study area. VanDijk (1973), however, indicated that saw-whet and boreal owls have the most strongly asymmetrical ears of all owls, and that screech and great-horned owls have "rather small and symmetrical ear openings without ear flaps." Whether these species rely on hearing or vision to different degrees is not

known. Differences in ear structure, though, do not lead to an obvious difference in activity among these species for screech as well as saw-whet and boreal owls are nocturnal in the RNRW.

Hildebrand (1974) discussed functional differences of various wing shapes and suggested that an elliptical wing provides maneuverability and precise control. These features are especially useful for an owl hunting in dense vegetation. A longer wing is more useful for sustained flight, but relatively larger wing areas lower the speed of most efficient flight.

The long-eared owl has a light wing loading and long wing (Table 19). These features are consistent with hunting on the wing in a slow coursing flight (Marti 1974). Saw-whet, screech, and boreal owls (forest species with similar food habits) have similar wing length indices; however, the saw-whet owl has lighter wing loadings. Forbes and Warner (1974) and my own information indicate the saw-whet owl hunts in denser forest cover than screech or boreal owls. Added maneuverability is therefore required. The lighter wing loading may also be better suited for transporting relatively larger prey.

The pygmy owl has a low wing length index. It takes a varied diet, whereas the flammulated owl, most similar in size, is completely insectivorous, and has a much longer wing. A small wing area may give the pygmy owl sufficient striking force to kill vertebrate prey but less lift for transporting

Table 19. Variation in wing structure of seven owl species.

$$\text{Wing Loading} = \frac{\text{Wing Area (cm}^2\text{)}}{\text{Bird Weight (g)}} ;$$

$$\text{Wing length index} = \frac{\text{Wing Cord (cm)}}{\sqrt[3]{\text{Bird Weight (g)}}} .$$

Owl Species	Wing Loading	Wing Length Index	Source
Saw-whet	3.88		Poole (1938)
Screech	1.87		'
Long-eared	5.13		'
Long-eared	4.22		'
Great horned	1.77		'
Great horned	1.64		'
Pygmy		2.29	Snyder & Wiley
Saw-whet		3.12	(1976)
Boreal		3.41	'
Screech		2.97	'
Great horned		3.18	'
Long-eared		4.42	'
Flammulated		3.44	'
Saw-whet	3.49	3.27	This Study
Screech	2.27	3.02	'
Boreal	2.51	3.24	'

the load. In winter, when vertebrate prey is most important, the owl doesn't have to transport prey long distances. More information is needed on the foraging behavior and comparative morphology of owls to completely understand partitioning of habitat and food resources by these species.

To summarize the niche pattern of these owls: 1) food and microhabitat niche are most important in resource segregation,

and 2) food niche differences most often are associated with differences in foraging time (diurnal-nocturnal) or microhabitat (Fig. 11).

	BOREAL	SCREECH	GREAT-HORNED	SAW-WHET
PYGMY	⊙	⊙	○	⊙
BOREAL		-	⊙	/
SCREECH			/	/
GREAT-HORNED				⊙

Symbol	Resource
-	Macrohabitat
/	Microhabitat
⊙	Time of Activity
○	Food

Fig. 11. Summary of resource dimensions most different in the niches of five forest cwls.

Function Of Niche Pattern

Is there any evidence that the pattern of resource utilization among the species results from competition? Schoener (1974) argued that competition should result in an over-dispersion of niches in niche-space recognized by: 1) the regular spacing of species along a single dimension, 2) increase in number of important dimensions with increase in species number, or 3) separation of species along

complimentary dimensions. Several owl species with similar utilization of one or two niche dimensions differ substantially on a third, i.e., they exhibit complimentary niche patterns. Most obvious is the flammulated owl. This species forages at the same time as boreal, saw-whet, and screech owls, and uses the same habitat as boreal owls. Insect prey which flammulated owls consume, however, is unutilized by any other owl. Boreal, screech, and saw-whet owls with similar food and temporal niches differ in macro and/or microhabitat. All three species consume mainly mammalian prey of the same size classes and all forage nocturnally. They appear to avoid competition by segregating in habitat niche-space.

The lower abundance of saw-whet owls at Chamberlain than Taylor may be due to harsher climate, fewer nest cavities, lower prey populations, or competition between the saw-whet and its congener, the boreal owl, which is not present at Taylor. The saw-whet owls' macrohabitat niche breadth is substantially reduced at Chamberlain, a phenomenon suggestive of either ecologic divergence due to competition or simply a response to less suitable habitat.

Mechanism for Resource Partitioning

By what mechanism do the owls avoid substantial niche overlap? Differences in niche may be due to: 1) direct interference competition (interspecific territoriality), 2)

exploitation competition (species a by utilizing resources makes those resources less valuable to species b), or 3) innate selection for different portions of the available niche-space. The first two situations would be expected to operate in cases of recent sympatry of ecologically similar forms (Orians and Willson 1964). Situation 3 may be the consequence of 1) and 2) operating over a longer period (Wecker 1964).

Both interspecific territoriality and exploitation competition should be manifest in habitat segregation. Territorial activity must be centered upon a defensible resource. Forest birds often defend space to secure nest sites or sufficient foraging areas. Energetically interspecific territoriality is very costly. Therefore only the most valuable habitats may be defended, and other species are allowed to exploit other usable but less valuable habitats. Likewise, optimal foraging theory predicts that as prey becomes less abundant in an individual's foraging area (as through exploitation of the resource by another species), the number of patch types (habitats) used should be reduced but the range of prey taken in a particular patch should remain unchanged (Orians 1971). Different morphologies and behaviors suggest that the optimum habitat of two species should differ, allowing coexistence through ecological divergence on the habitat niche. The third mechanism for resource partitioning, innate selection, may result in different foraging periods, different food size or type, or different habitat use.

Speculation on the mechanisms of resource partitioning among the forest owls I studied is difficult but may stimulate further thought on the subject. Saw-whet and great-horned owl, boreal and flammulated owl, and boreal and pygmy owl individuals were observed in close proximity without antagonistic interactions. Strong evidence for interspecific territories among other species pairs is lacking, however congeneric saw-whet and boreal owls were not observed closer than 0.4 km and showed significant habitat segregation in the discriminant analysis. Many owl species are territorial so the apparatus for interspecific territoriality is generally available and would be expected most among closely related species which are ecologically and morphologically similar.

Owls with similar diets and foraging periods may be expected to partition resources through habitat segregation resulting from exploitation competition. Saw-whet - screech owl interactions may be an example. The saw-whet owl seems to avoid some suitable riverbottom habitats which the habitat specialist, screech owl, exploits more effectively.

With time, coexistence may lead to the innate recognition of species specific optimal habitat, or to divergence in foraging time and diet. The diurnal foraging of pygmy owls (a species morphologically adapted to nocturnal hunting as indicated by ear and eye structure) and the diet of flammulated owls are examples of this type of ecological divergence.

Limits On Distribution and Population Density

What factors likely limit the geographic distribution and abundance of forest owl species in the RNRW? Although owls were not censused to estimate population densities, several gross patterns observed in the RNRW are of interest. Screech owls inhabit only the deciduous habitats bordering Big Creek at Taylor; they are not found at Chamberlain. Within this narrow band of riparian habitat the screech owl is the most abundant owl. Conversely, the boreal owl, possibly the most abundant species at Chamberlain, is not found in lower life zones at Taylor. Although lodgepole pine habitats predominate at Chamberlain, boreal owls use the more open, mature, mixed conifer stands and the forest openings. Saw-whet owls are relatively abundant at Taylor, where they occupy all topographic positions and use a variety of habitats. At Chamberlain they are less abundant and commonly use lower topographic positions. Finally, the combined density for all owls is lower at Chamberlain than at Taylor.

Five of seven owl species found in the RNRW nest in tree cavities. The largest species, great-horned and long-eared owls nest on existing stick nests or cliff ledges. I did not survey the available nest structures and cannot assess the degree to which nest sites limit the distribution and abundance of the owls. However, diurnal raptors, whose nests

great-horned and long-eared owls often use, are rare throughout the study area. Black-billed magpies (Pica pica), which also build large stick nests, are common only at lower elevations. Conceivably, great-horned and long-eared owl abundance and distribution may be limited by the paucity of nest sites.

Nest cavities in the extensive lodgepole pine stands at Chamberlain are rare due to the small diameter of the trees and shallow sapwood (Bull 1980). In the mixed conifer habitats used by boreal owls, however, ponderosa pine and Douglas fir snags were common. Piliated and hairy woodpeckers, common flicker, and Williamson's sapsucker excavated a variety of cavity sizes in these snags. Cavity availability in particular areas, then, may limit habitat use by boreal owls. Within the mixed conifer habitat, however, cavities should not limit boreal owl abundance. The role of cavity availability in limiting pygmy, saw-whet, and flammulated owl abundance and distribution at Chamberlain may be similar. Douglas fir is the only tree species that occurs at Taylor, except along stream courses where black cottonwood and rare aspen or Ponderosa pine are available. Thin sapwood and decay resistant heartwood of Douglas fir discourage excavation by primary cavity nesters (Bull 1980). Natural cavities form readily in cottonwood, however, and may preclude the need for of primary excavators. Therefore cavities for screech owls may be locally abundant in scattered stands of cottonwood. Saw-whet and pygmy owls, which rely on cavities in Douglas fir, may experience lower

availability of nest sites. Abundance of large diameter snags in the uncut forest, however, may compensate for poor snag quality. Pileated and hairy woodpeckers and common flicker all occur at Taylor and excavate a variety of cavity sizes.

MacArthur (1972) suggested that whereas climate often limits the northern distribution of birds, competition determines the southern boundary for many temperate species. The truncated elevational distribution of boreal and screech owls may be explained in a similar way. Screech owl distribution appears to be strongly influenced by habitat, but, the severity of winter weather and subsequent prolonged snowcover and cold may determine its upper elevation limit. Boreal owl populations in Idaho represent peninsular or refugium groups occupying suitable high elevation habitat well south of northern contiguous populations. At lower elevations competition with abundant saw-whet and screech owls may limit the distribution of boreal owls. Continental distribution for both species of Aegoleus is widespread; ranges extend from coast to coast (Godfrey 1966). Northern saw-whet and southern boreal owl breeding distributions overlap little, in agreement with MacArthur's (1972) hypothesis for ecologically and morphologically similar species. Likewise, eastern screech owl and boreal owl distributions meet near the southern Canadian border with little overlap (Eckert and Karalus 1974). Boreal owl abundance at Chamberlain may be limited by both food and habitat. The species uses only a portion of the available

habitats. Those areas without suitable nest cavities or vegetation structure are not used. The clutch of just two eggs discovered at Chamberlain may indicate that food was limiting for this pair. Four to six eggs are common clutches for boreal owls. Southern (1970) interpreted breeding success as a measure of prey availability for tawny owls in England.

Saw-whet, great-horned, and pygmy owls exist at both Chamberlain and Taylor. The abundance of saw-whet owls at Chamberlain may be limited by competition, climate, or food. Only 1/2 the size of boreal owls, the saw-whet owls may suffer sooner during periods of prey scarcity under conditions of severe winter weather. Graber (1962) noted that even when one considers the elevated basal metabolic rate expected for size differences, saw-whet owls have relatively higher metabolic rates than long-eared and short-eared owls (Asio flammeus). Boreal owls, then, may limit the habitats used by saw-whet owls, whereas climate and food interactions could further limit abundance.

Great horned owl abundance, I feel, is probably limited by a combination of available prey, habitat, and nest sites. Great horned owls are restricted from hunting in dense vegetation because of poor mobility. Within huntable habitat, scarcity of cottontail, hares, and other large prey may limit owl abundance as demonstrated by Rusch et al. (1972) for horned owls in Canada.

CHAPTER TWO: ROOST HABITAT SELECTION

Abstract: Roost sites chosen by radio-tagged boreal, saw-whet, and screech owls were examined during winter, spring, and summer to compare species roosting behaviors. Roosts used by individual boreal and saw-whet owls were dispersed throughout their home range. Individual screech owls often returned to preferred roost sites. One boreal owl roost was located in a snag, and one saw-whet owl roost was in deciduous cover. Otherwise, these species roosted in coniferous trees. Screech owls often roosted in deciduous shrubs following leafout in spring.

The amount of protection afforded by roost sites varies among the three species. Boreal owls roosted in situations that provided less protection immediately above the bird. Saw-whet owls roosted much further from the tree bole than the other species. I propose that for the owls studied, roost sites are chosen to provide protection from predators moreso than for thermal economy.

INTRODUCTION

Thermal economy and predator avoidance are important during a bird's inactive period. Roost sites, then, should protect the bird from wind and precipitation, offer a microclimate closer to thermalneutral than average ambient temperatures, and conceal or guard the bird from predators. Either extreme environmental conditions or keen predation pressures may cause a bird to make roost choices in accordance with the more pressing need.

Balda et al. (1977) explained roost selection and posturing in pinion jays (Gymnorhinus cyanocephala) in terms of thermal regulation as well as predator detection and avoidance. The jays roosted on the warmer side of trees and made seasonal adjustments in roost height in response to the amount of heat radiated by the ground. Perch location, posture before roosting, and open flock structure in the communal roost all appeared to reflect predator avoidance. Barrows (1981), found that physical features associated with summer roosts of spotted owls created a microclimate 1-6° C cooler than adjacent, more open areas.

Bondrup-Nielsen (1978:138) studied boreal owls in the northern boreal forest of Canada and concluded that "within a

habitat, there appeared to be very little choice [exhibited] in roost site selection based on the parameters measured."

In 1981 I examined roost sites of boreal and saw-whet owls during winter and spring and of screech owls during late winter, spring, and summer. Characteristics of the vegetation around the roost site and the position of the owl in the tree were used to compare the roosting habits of these three small forest owls.

METHODS

Radio tagged boreal, saw-whet, and screech owls at the Taylor Ranch and Chamberlain Basin study sites were located on their diurnal roosts. Locations of all roosts were recorded on maps and aerial photographs, and flagged for relocation. The position of the owl in the roost tree was recorded by height above ground (using a clinometer), distance from bole, and distance to nearest branch above and below the roost. The amount of cover afforded the owl by vegetation above, to the sides, and below the roost was rated on a scale from one to five for each direction. Both the density of vegetation and distance to the protective cover was used in assigning the cover rating.

The roost tree was later characterized by height, DBH, and

minimum canopy height. Timber density within two concentric circles around the roost (5.2 m (16.92 ft) and 11.4 m (37.25 ft) radius) was recorded in four size classes (1-3, 3-9, 9-21, and >21 inches DBH). A modified line intercept sample totaling 366 m (1200 ft) was used to characterize the structure of surrounding vegetation. I measured the portion of 8 lines, radial to the roost, intercepted by five vegetation cover categories. The categories were nontimbered, conifer shrub, pole timber, mature timber, and bottomland. Lines in the four cardinal directions each measured 61 m (200ft); the remaining four lines were each 30 m (100 ft (Fig. 12)).

Data was tested for normality. Those variables deviating significantly from a normal distribution were transformed and retested. Statistical tests were performed on the transformed data.

RESULTS

Roosts of one boreal, two screech, and three saw-whet owls were located through radio tracking. From these birds I was able to locate 13 boreal owl roosts between 26 January and 8 April, 15 saw-whet roosts between 12 March and 22 June, and 8 different screech owl roosts between 11 February and 5 August. Only a single boreal owl roost occurred in a cavity; on all

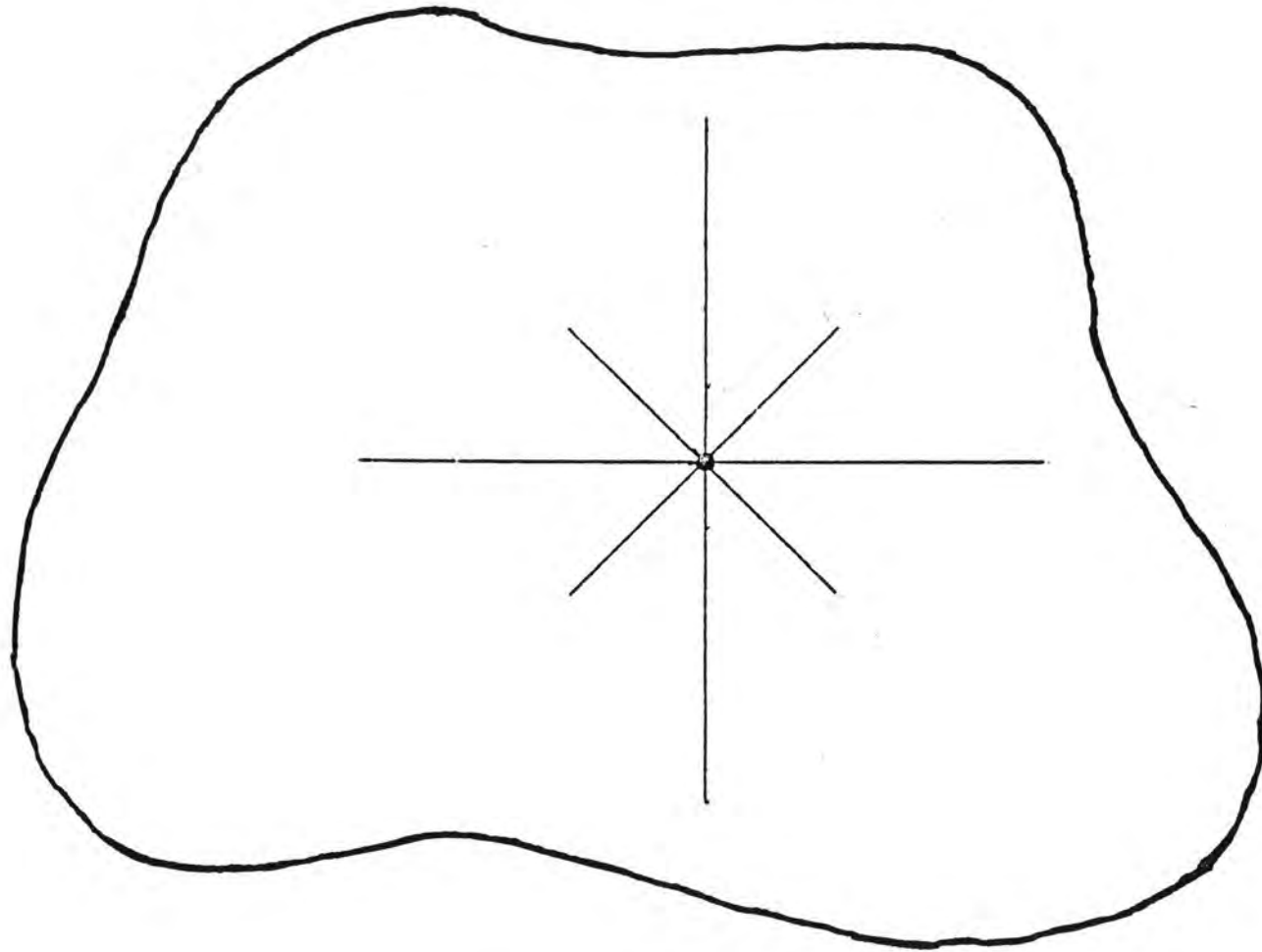


Fig. 12. Sampling pattern used to assess degree of vegetation heterogeneity for nest and roost sites.

other occasions owls roosted in conifers or shrubs. Only screech owls showed repeated use of roosting perches. One screech owl used the same roost on 3 of 4 occasions. Seven pellets found under one boreal owl roost, however, indicated repeated use by this bird. Roosts of boreal and saw-whet owls were dispersed. On consecutive days roosts were separated by as much as 2 and 1.8 km, respectively.

Roost Site Characteristics

Roost Tree

All roost trees of the boreal owl were coniferous, and its home range less than 2% deciduous cover. Home ranges of three saw-whet owls were bisected by stream courses and associated deciduous riparian habitat. A single saw-whet owl roost was found in a deciduous thicket; all others occurred in coniferous trees. Both screech owls concentrated their activity along Big Creek where conifer and deciduous habitats are mixed. Prior to leafout in spring, only conifers were used; however, after leafout, 45% of the screech owl roosts were in deciduous cover.

Over 80% of the boreal and screech owls perched immediately next to the bole of the roost tree. In contrast, 54% of the saw-whet owl roosts were greater than one meter from the bole (Table 20). Saw-whet owls often perched within foliated portions of the tree on the outer half of the branch.

The protection offered the roosting owl by surrounding

Table 20. Characteristics (mean (S.E.)) of roost trees used by three owl species in the River of No Return Wilderness, Idaho.

Characteristic	Owl Species		
	Boreal	Saw-whet	Screech
Roost height, ft	22.5 (1.96)	13.6 (2.09)	15.1 (4.79)
Min. roost height, ft	9	3	2
Max. roost height, ft	35	24	40
Roost tree height, ft	63.6 (5.30)	74.0 (9.99)	69.4 (15.22)
Canopy height of roost tree, ft	16.9 (2.94)	5.8 (0.87)	7.4 (3.26)
DBH of roost tree, in	14.2 (2.30)	18.1 (3.23)	21.3 (5.65)

Table 21. Kruskal-Wallis analysis of cover at roosts for three owl species. A significant result indicates a difference between the species in protection provided by the roost.

Direction of Cover	Kruskal-Wallis H	p-Value
Above roost	5.847	0.054
Below roost	0.277	0.87
Sides of roost	1.96	0.38

foliage appeared to differ between species. The boreal owl was much easier to find on its roost than the saw-whet or screech owls. After locating the roost tree using the radio signal, we could usually find the boreal owl within 10 minutes: finding saw-whet and screech owls took up to 45 minutes. Nonparametric ANOVA (Kruskal-Wallis test, Daniel 1978) of the cover rating above, below, and to the side of the roost indicated a difference between species in protection above the roost (Table 21). Boreal roosts had the least protection from above, and saw-whet owls the most protection. There was no significant difference among species in distances to the nearest branch above or below the roost (ANOVA; $p = 0.16$ above, and $p = 0.21$ below). Perch positions of all three species afforded less cover below than above. I believe that this provided a view of the ground below.

Surrounding Vegetation

Tree density was higher around boreal owl roosts than either saw-whet or screech owl roosts (Table 22). Multivariate ANOVA, by study site, however, demonstrated that the apparent greater timber density around boreal owl roosts resulted from differences in habitat at Chamberlain and Taylor Ranch rather than differences in roost selection by the owl species. Boreal owls chose roosts with denser timber within 5.1 m of the roost than in the next 6 m (paired-t test $p = 0.001$). For the saw-whet and screech owls, the higher timber density near the

Table 22. Mean (S.E.) density of trees near roosts for three owl species. Density is expressed in stems per 0.01 acre.

Distance of trees from roost	Timber size class (in)	Owl Species		
		Boreal	Saw-whet	Screech
5.1 m	1-3	2.73 (0.810)	1.23 (1.645)	2.63 (1.639)
"	3-9	2.38 (0.549)	1.77 (0.842)	1.56 (0.988)
"	9-21	0.88 (0.241)	0.07 (0.045)	0.06 (0.063)
"	21	0.08 (0.052)	0.07 (0.045)	0
"	All sizes combined	6.08 (0.914)	3.13 (1.461)	4.25 (2.338)
5.1 - 11.3 m	1-3	1.46 (0.356)	0.35 (0.136)	0.69 (0.552)
"	3-9	1.46 (0.333)	0.68 (0.341)	0.88 (0.678)
"	9-21	0.55 (0.081)	0.13 (0.031)	0.03 (0.020)
"	21	0.02 (0.013)	0.02 (0.011)	0
"	All sizes combined	3.63 (0.548)	1.20 (0.467)	1.61 (1.222)

roost was not significant (paired-t test $p = 0.09$ for both species).

Analysis of the vegetation cover (proportions of major categories) within a 60.5 m radius of the roost showed no significant overall differences between owl species (MANOVA $p = 0.11$ at Taylor Ranch, $p = 0.14$ at Chamberlain).

DISCUSSION

Major differences between roost sites of boreal, saw-whet, and screech owls were in the amount of cover above the roost and position of the perch on the branch. Both characteristics relate to protection or concealment, and serve to reduce exposure to predators and extreme weather conditions.

Relationships between roost selection and thermoregulation in winter have been quantitatively studied in the American Robin (Turdus migratorius) (Walsgerg and King 1980) and starling (Sturus vulgaris) (Kelty and Lustick 1977). Both species roost in dense vegetation to reduce radiative heat loss to the sky. Convective heat losses are also lower because of reduced wind velocities experienced on the roost. Air temperatures, however, are not significantly lower than those experienced in open conditions nearby. The authors estimated metabolic savings of 3-5% for the robins and 12-38% for the

starlings compared to birds roosting without cover. Differences in these estimates resulted mainly from differences in wind shielding provided at the roost. Walsberg and King (1980) noted that the robins roosted in the foliage toward the end of the branch. By roosting next to the tree trunk, however, the greater wind protection would have increased metabolic savings to 20%. The authors suggested that roost selection for these robins may reflect protection from predators rather than thermal economy.

In my study, the higher density of trees immediately around the owl roosts suggests that thermoregulative economy may be gained from the owl roost selection through reduced wind speeds. However, the small saw-whet owl roosted in the foliage toward the end of the branch where Walsberg and King (1980) noted only moderate reduction in wind speed. The larger boreal and screech owls, whose silhouettes would be more conspicuous far out on the branch, roosted next to the trunk where their cryptic plumage matched the tree bark. None of the owls perched on the unprotected area between the bole and the foliage.

Ligon (1967) and Calder and King (1974) suggest that nocturnal activity is thermally economical. Waste metabolic heat from activity is used for thermal regulation during the cold night, and roosting occurs during the less stressful daytime period. Ligon (1969) also notes the heavy insulation provided by saw-whet and northern screech owl plumage.

Compared to passerines, then, the need to choose roost sites for thermal economy should be less for these owls. Characteristics of roosts selected by the owls imply that predator avoidance is at least as important as thermal economy. Each species chose perches which provided concealment at the possible expense of lower thermal economy.

Roosting in a cavity should provide maximum thermal economy and protection from avian predators. Kendeigh (1961) estimated an 11.1% metabolic savings by a house sparrow (Passer domesticus) roosting in a nest box based solely on the difference in temperature within and outside the box. Complete shielding from wind, as estimated by Walsberg and King (1980), would reduce energy expenditure 20% more. Balda et al. (1977) suggests that species commonly roost in situations similar to their nest site; species which nest in cavities or domed nests would select similar roost situations. Why didn't the boreal, saw-whet, and screech owls roost in cavities?

Perhaps owls consistently roost in cavities only when sufficient protective cover for concealment is not available. VanCamp and Henny (1975) reported that screech owls in deciduous forests began roosting in nest boxes during October when leaf fall would make a roosting owl most conspicuous. Roosting owls should not be as conspicuous in coniferous forest environments. Cavity availability should not have limited the use of cavities for roosting in the ENRW as the sedentary owls occupied their breeding territory by mid-winter and snags were

plentiful in the unharvested forest.

I suggest that a cavity-roosting owl may be protected from aerial predators but vulnerable to marten (Martes americana) or other arboreal mammals. Roosting under a conifer may provide adequate concealment from hawks and other owls and the opportunity to escape approaching mammalian predators. Finally I hypothesize that for a sedentary owl, the problems of roost-nest sanitation would discourage development of cavity roosting behavior. Kilham (1971) noticed daily roost sanitation by white-breasted nuthatches (Sitta carolinensis) removing feces each morning. Owls on the other hand have extremely liquid feces and cleaning the cavity might be difficult. The cost of increased ectoparasites and fouling of the nest cavity as a result of roosting may outweigh benefits of thermal economy and predator concealment to an owl with adequate tree roosts available.

CHAPTER THREE: MOVEMENTS AND HOME RANGE SIZE

Abstract: I captured and radio tagged several saw-whet, boreal, and screech owls in the River of No Return Wilderness, Idaho to study seasonal movement patterns. Evidence suggests that all three species are non migratory. Saw-whet owls appear to occupy and defend exclusive nesting territories. I present results of three methods of home range estimation for three saw-whet, two screech, and one boreal owl.

INTRODUCTION

Forest owl species of temperate climates vary in their seasonal movement patterns. Adult great horned (Baumgartner 1939, Craighead and Craighead 1969), barred (Nicholls and Warner 1972), Ural (Lundberg 1979), tawny (Southern 1970), and screech owls (Craighead and Craighead 1969, VanCamp and Henny 1975) remain within a single home range throughout the year. These species are monogamous and pairs remain together on the territory for more than one year.

Long-eared owls (Lundberg 1979), flammulated owls

(Phillips 1942), and the saw-whet owl in eastern North America (Holroyd and Woods 1975, Weir et al 1980) are migratory. Mysterud (1970), Lundberg (1979), and Wallin and Andersson (1981) consider the boreal owl in Europe nomadic, because it remains sedentary during periods of prey abundance but moves when prey becomes scarce. Lundberg (1979:278) believes, however, that while female and young boreal owls migrate, "males, to the extent that they possess favorable territories, are resident". For this relatively short-lived species, migratory behavior is favored in response to food shortage. An individual that remains sedentary during years of prey shortage will miss the opportunity to breed and possibly die before prey is plentiful. By moving during prey shortages, a new habitat with sufficient prey to allow breeding might be located. The scarcity of adequate nest cavities, however, forces the male to forgo breeding and defend the cavity for future breeding attempts.

Generally, forest owls are considered territorial. During the breeding season they defend an area which contains the nest site. Territorial behavior is well documented in great horned (Baumgartner 1939), flammulated (Marshall 1939), and tawny owls (Southern 1970). Southern's (1970) comprehensive study of a tawny owl population suggests that a territory functions to assure the pair of adequate food to breed and overwinter. Familiarity with the territory enables the birds to locate sufficient prey in periods of extreme scarcity. The

territorial behavior seems to result in a degree of population regulation by allowing young owls to fill space vacated through adult mortality while forcing excess young to disperse or starve.

I studied movements and territorial behavior of saw-whet, boreal, and screech owls from January through July, 1981 in the RNRW, Idaho. The objectives were to determine the aerial extent of owl home ranges and whether or not the birds were sedentary.

METHODS

Trapping

Bal-chatri traps and mist net sets were used to capture boreal, saw-whet, and screech owls. The quonset shaped cage of the bal-chatri trap modified from Ward and Marten (1968) measured 14 cm wide and 18 cm long and was constructed from 1.4 cm. (1/2 in) wire-mesh. The base, larger than the cage, was 30 cm square. The false top, supporting nylon nooses, was constructed from chicken wire. Nooses of 2.7 kg test monofilament line were knotted to the base and false top as described by Jenkins (1979). One or two wild deer mice were placed in the cage along with dried leaves to attract the owls.

Five traps were set along the owl survey route each evening and retrieved 1-4 hours after dark. When possible, I placed traps near any owls heard singing.

Mist net sets were placed close to singing locations of owls heard the previous night. Black, 2 by 13 m, 5.5 cm mesh nets were stacked 3-high and placed in a narrow aisle of the forest where low branches provided potential perches on either side. A model owl decoy was placed in a tree on one side of the net; an assistant and I sat on opposite sides of the net. At dark a tape recorded owl call was played. When the owl flew nearby, the assistant and I alternated calling to make the owl fly across the aisle and into the net.

Radio-tagging

I used 7 and 10.5 g radio transmitters with 19.5 cm whip antennas purchased from Wildlife Materials Inc. Pulse rate was set near 60 pulses per min. with a pulse width of 18 milliseconds and signal strength of near -24 dBm. I initially used a tail mount so that radios would be shed in late summer molt. Also, the risks of restricting wing motion and abrasion caused by a backpack mount were avoided. Bray and Corner (1972) had seen no behavior restrictions in two male American kestrels (Falco sparverius) with 8 g tail mounts. I attached the radio dorsally to the two central rectrices with Ducco cement. The saw-whet and screech owls lost the two center

rectrices with attached radio in 2 to 7 days. One female boreal owl shed a tail mounted 7 g radio after 73 days. We then changed to dorsally mounted transmitters. Radios were mounted directly between the wings, and glued to the contour feathers for stability. Rubber tubing around the bird's wings held the transmitter firmly in place. This backpack mount proved satisfactory. One saw-whet owl had lost 5 g after 52 days with a 7 g backpack mounted transmitter and another had gained 6 g after 24 days.

Radio Tracking

Owls were located on their daytime roosts at irregular intervals from one to 50 days apart. I recorded locations on a 1:24,000 topographic map. On several occasions I located the birds at night while they foraged. Unlike the roost locations the bird was not seen while foraging, and therefore, the precision of the location may be questioned. However, I did not rely on ordinary triangulation for foraging locations, rather I approached the owl very close (judging from signal strength) and felt these locations were within 30 m of the true location.

Analysis

The most rigorous analysis involved determining the size of each birds home range. Only one foraging location per night was used in the analysis to ensure independence of observations. Daytime roost and nighttime foraging locations from the same day were considered independent as the foraging location was recorded at least an hour into the night, after the bird had been foraging for a while.

Several methods of home range estimation were used, (program HOME RANGE, Samuel et al. 1983) including: 1) minimum convex polygon (a non-statistical method), 2) Jennrich and Turner's (1969) bivariate normal ellipse, 3) a modified Jennrich-Turner estimate in which any 'outlier' locations are given a reduced weight, and 4) a modified estimate of the area representing a particular proportion of the animals utilization volume (Dixon and Chapman 1980). For a complete discussion of these techniques see Samuel and Garton (in review) and Samuel et al. (1983).

The minimum convex polygon is the most common home range method encountered in current literature, and is provided here for comparison. The statistically based methods, however, give a more realistic estimate of the area used by an animal. I tested an assumption of the Jennrich-Turner (1969) and minimum convex polygon estimates by comparing the spatial distribution

of sample locations against bivariate normal and bivariate uniform distributions. Significant differences from these distributions indicate that the Jennrich-Turner (bivariate normal) and minimum convex polygon (bivariate uniform) estimates of home range are not appropriate, and that Dixon and Chapman's (1980) measure should be used.

RESULTS AND DISCUSSION

Trapping Success

A mated pair of boreal owls was captured on bal-chatri traps. The female was recaptured once in a bal-chatri trap and again by hand from inside the nest cavity to replace her radio package. Of three screech owls captured; one was captured twice on bal-chatri traps, a male (based on nesting behavior) was called into a mist net, and a weak flying young bird caught by hand. The young bird was recaptured using a bal-chatri trap. Four saw-whet owls were drawn into mist nets by tape recorded calls. One was recaptured on a bal-chatri trap, and two others recaptured on their roosts by hand.

Bondrup-Nielsen (1978) and my own experience indicated that boreal owls could probably be captured by calling them into mist nets but not as easily as saw-whet owls. Screech

owls never approached us in response to taped calls; the single bird captured in a mist net required 2 nights effort. Screech owls are probably most easily captured by placing a bal-chatri trap near a calling bird (Smith and Walsh 1981). Our placement of bal-chatri traps beneath singing saw-whet owls, failed to produce any new captures. During the late February - mid April, singing period, saw-whet owls respond aggressively to imitated calls played near their calling perch. During this period, over 50% of our attempts to capture saw-whet owls in mist nets were successful.

Territorial Behavior in Saw-whet owl

I witnessed no aggressive encounters between saw-whet owls. My observations, however, suggest that territoriality occurs during the courtship and early breeding, and possibly at other periods. The owls responded to imitated calls near their singing perch by flying at me or back and forth over my head. I interpreted this as aggressive behavior. Owls usually flew directly toward my head as I whistled the saw-whet call to attract them into the mist net. On two nights, we set a mist net between two calling owls that were separated by about 60 m. Their calling had been heard in the area for a couple weeks. I was unable to attract either owl into the net with imitated calls. Rather, on both nights, one bird soon flew further away and continued calling. I hypothesize that I was positioned at

a pre-established border between the owl territories and neither bird was compelled to respond because I was not invading the core of its territory.

Migratory Status

Two factors suggest that boreal, saw-whet, and probably also screech owls are permanent residents in the RNRW: the dates of territorial calling in relation to other records of migration, and site tenacity exhibited by some individuals. Table 23 lists the date when individuals of each species were first heard calling during the winters of 1980 and 1981 in the RNRW. Because I moved between three field camps and boreal, screech, long-eared, and flammulated owls were not found at all camps, these species may begin calling earlier than shown.

In eastern North America, saw-whet owl migration occurs from 1 March to 31 May (Holroyd and Woods 1975). In contrast I had located 13 calling saw-whet owls by 1 March 1981 (Table 23). Calling by all species in the RNRW except the flammulated owl began in early to mid February. I saw no indication that early calling birds were passing through the region; continuous calling was heard from early spring throughout the courting period within the same areas. I conclude that these saw-whet owls, unlike the eastern populations, are non-migratory.

A female boreal owl provides further evidence of a sedentary population. This owl, radio-tagged on 24 January,

Table 23. Earliest date that seven owl species were first heard calling on two years in the River of No Return Wilderness, Idaho.

Species	Date First Heard	
	1980	1981
Saw-whet	9 February	7 February
Screech	22 February	5 February
Boreal	26 February	1 March
Great horned	11 February	2 February
Pygmy	2 March	7 February
Long-eared	5 February	7 February
Flammulated		1 June

1981, stayed in the same home range and bred in April.

Although saw-whet owls did not appear to be migratory (in the sense of moving in and out of the study area), they may change elevations through the year. Saw-whet singing at the highest elevations occurred relatively late in spring compared to other owl species. I hypothesize that some saw-whet owls may breed at high elevations and move to lower habitats during winter.

Individual Home Ranges

Home range size for the six owls in the RNRW ranged from 7 to 556 ha (Table 24). The minimum convex polygon,

Table 24. Home range areas (ha) of six owls in the River of No Return Wilderness, Idaho, estimated by four different methods.

Owl	Sample size		Sign. diff. bivariate normal		Sign. diff. bivariate uniform ³	Jen-Turner home range ⁴	Weighted non-circular home range ⁵	Minimum convex polygon	Dixon and Chapman (1980) ⁶	
	Foraging	Roosting	Jen-Tur ¹	Weighted J-T ²					75% contour	95% contour
Screech - 22	4	4	*	*	*	22 (47)	7 (16)	7	3	9
Screech - 25	7	11	*		*	22 (48)	16 (34)	18	29	58
Saw-whet - 44	4	5	*	*		22 (47)	16 (34)	14	8	16
Saw-whet - 54	2	4		*		257 (556)	171 (371)	93	59	129
Saw-whet - 41	1	5		*		53 (116)	34 (74)	17	13	27
Boreal - 21	7	11	*	*	*	35 (76)	20 (43)	32	33	46

¹ Samuel and Garton (in review). Highlighted cases reject the assumption of normality required for the home range estimate using Jennrich and Turner's (1969) method.

² Samuel and Garton (in review). Highlighted cases reject the assumption of normality required for the home range estimate using the weighted non-circular home range method.

³ Highlighted cases reject the assumption of a uniform distribution required for the home range estimate using the minimum convex polygon.

⁴ Jennrich and Turner's (1969) home range estimate, 75% and (95%) probability ellipse.

⁵ Samuel and Garton (in review), Non-circular home range estimate, 75% and (95%) probability ellipse.

⁶ Using program by Samuel et al. (1983).

Jennrich-Turner (1969) and weighted non-circular (Samuel and Garton in review) home range areas are generally smaller than reported for other small owls. However, if the bivariate uniform or bivariate normal tests are significant, these areas should not be considered reliable. Seventy-five percent and 95% contours based on Dixon and Chapman's (1980), and Samuel et al.'s (1983) method may be the most reliable index of the area used intensively by the owl.

Problems of small sample sizes must be recognized for all six owls. Therefore, removal of any one location from a home range estimate will change the calculated area significantly. The majority of locations represent roost sites. Areas used for foraging were not always completely contained within areas used for roosting. The home ranges determined are therefore conservative; the actual areas used during the period may be larger.

I will briefly discuss each individual to emphasize the problems with the estimated home ranges. Please note that because the radioed owls were at different study camps I was unable to follow any individual continuously.

Boreal - 21 (Fig. 13), radio tracked 24 January till 14 June

This owl was identified as a female based on comparisons with the size of its mate, and nesting behavior. The owl's behavior changed with the onset of nesting as her activities were confined to the nest cavity. Therefore, I eliminated

nesting season locations (all were at the nest tree) and estimated her pre-nesting home range. In addition, during early February and again in early March she left her normal home range for several days. Only one accurate location, 1.7 km from the nearest location, was made during these excursions (Fig. 13). This 'outlier' location is not included in home range calculations. Including this point in the minimum convex polygon estimate raises the area to 73 ha. Anomalous movements just prior to breeding, also seen in mountain lions (Hornocker 1970), may be a means of assessing the surrounding habitat and owl population.

Screech - 22 (Fig. 14), radio tracked 10 - 26 Feb.

Unlike other owls I observed, this bird consistently returned to the same tree to roost. On 2 March, twenty days after being captured, it left its home range. The owl lost its two center rectrices and radio 5.5 km from the nearest location. Its final location is not included in home range calculations. The small sample size, clumping of roost locations, and lack of foraging locations result in a poor home range estimate. This bird does, however, demonstrate that screech owls will consistently use a single roost.

Screech - 25 (Fig. 15), radio tracked 29 April until 18 August

This bird was mated and fledged at least three young by mid June. During the nesting period the bird roosted in bushes

and trees, but never at the nest site, indicating it was a male. While foraging, this owl moved back and forth across the territory and we were unable to determine the location of the nest cavity from the owl's movements.

The distribution of locations was not significantly different from a bivariate normal distribution so both the Jennrich-Turner (1969) and weighted noncircular home range estimates are valid. A number of foraging as well as roosting locations were obtained, so the estimate of home range size is reliable for the nesting period.

Saw-whet - 44 (Fig. 16), radio tracked 23 March until 15 April.

This bird was heard calling for several weeks before being captured and appeared to have established a territory. Unfortunately the owl died 3 weeks after being captured when it impaled itself on a branch of a shrub. It appeared the owl was attacking prey when a branch 0.3 m from the ground became lodged between the transmitter and the owl's back.

Saw-whet 54 (Fig. 17), radio tracked 28 April until 4 August

This owl was heard calling (and captured) late in the spring after the majority of saw-whet owls had ceased singing. The owl's roosts were widely scattered and on several days I could not detect a radio signal. These characteristics indicated the bird may have been an unmated individual wandering over an enlarged home range. The eastern portion of

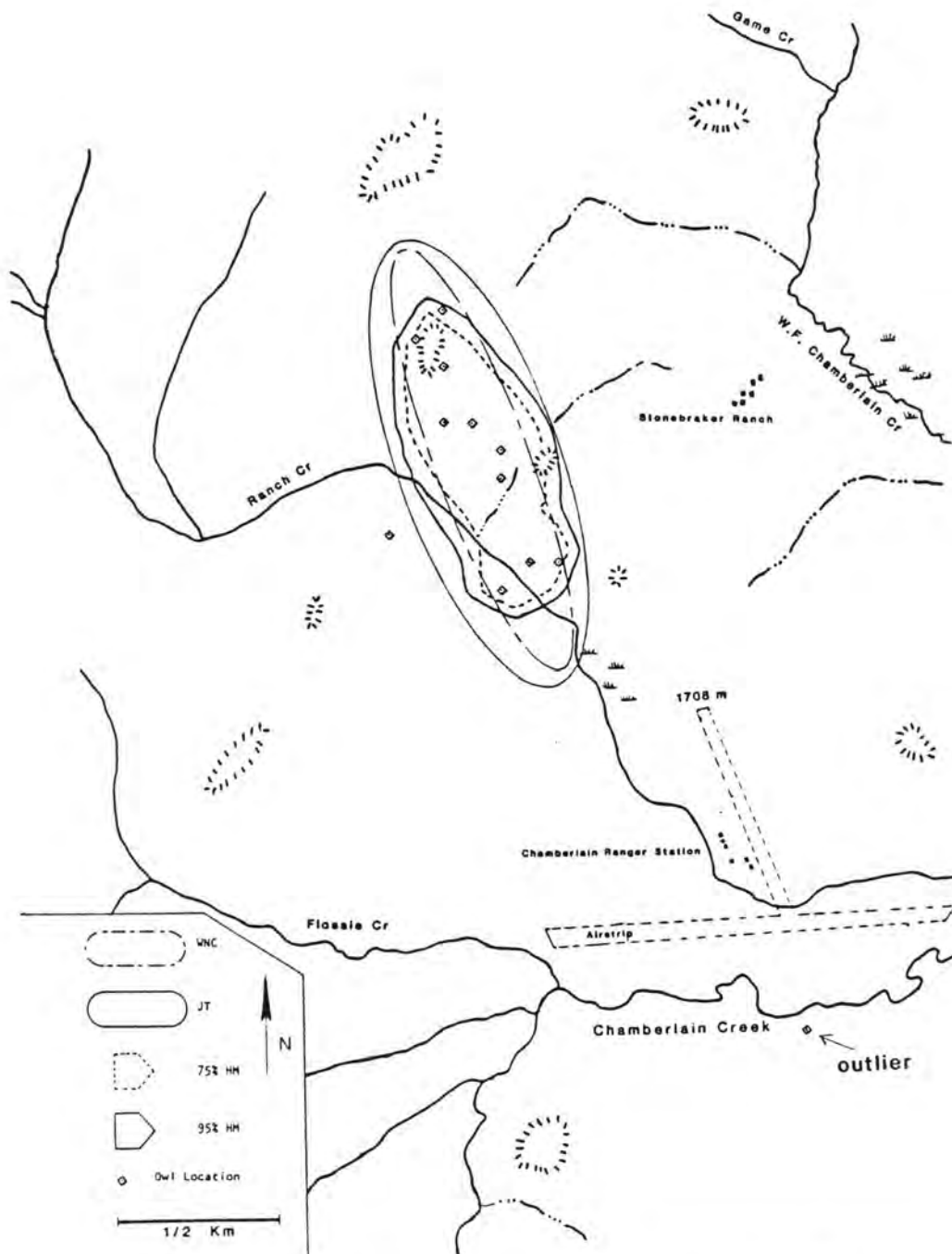


Fig. 13. Home range area of Boreal Owl - 21 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% bivariate confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HH) using the program by Samuel et al. (1983).

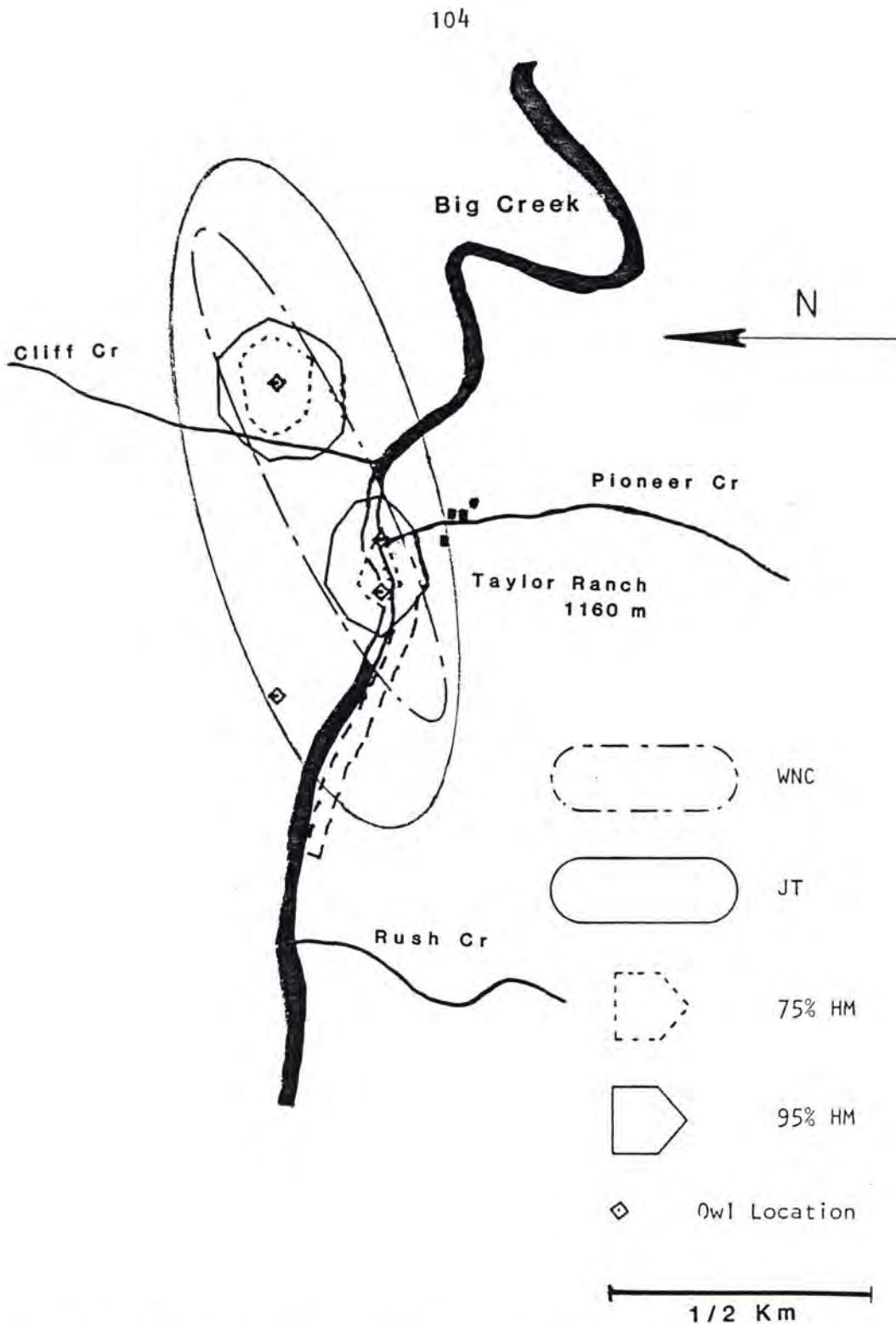


Fig. 14. Home range area of Screech - 22 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% bivariate confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HM) using the program by Samuel et al. (1983).

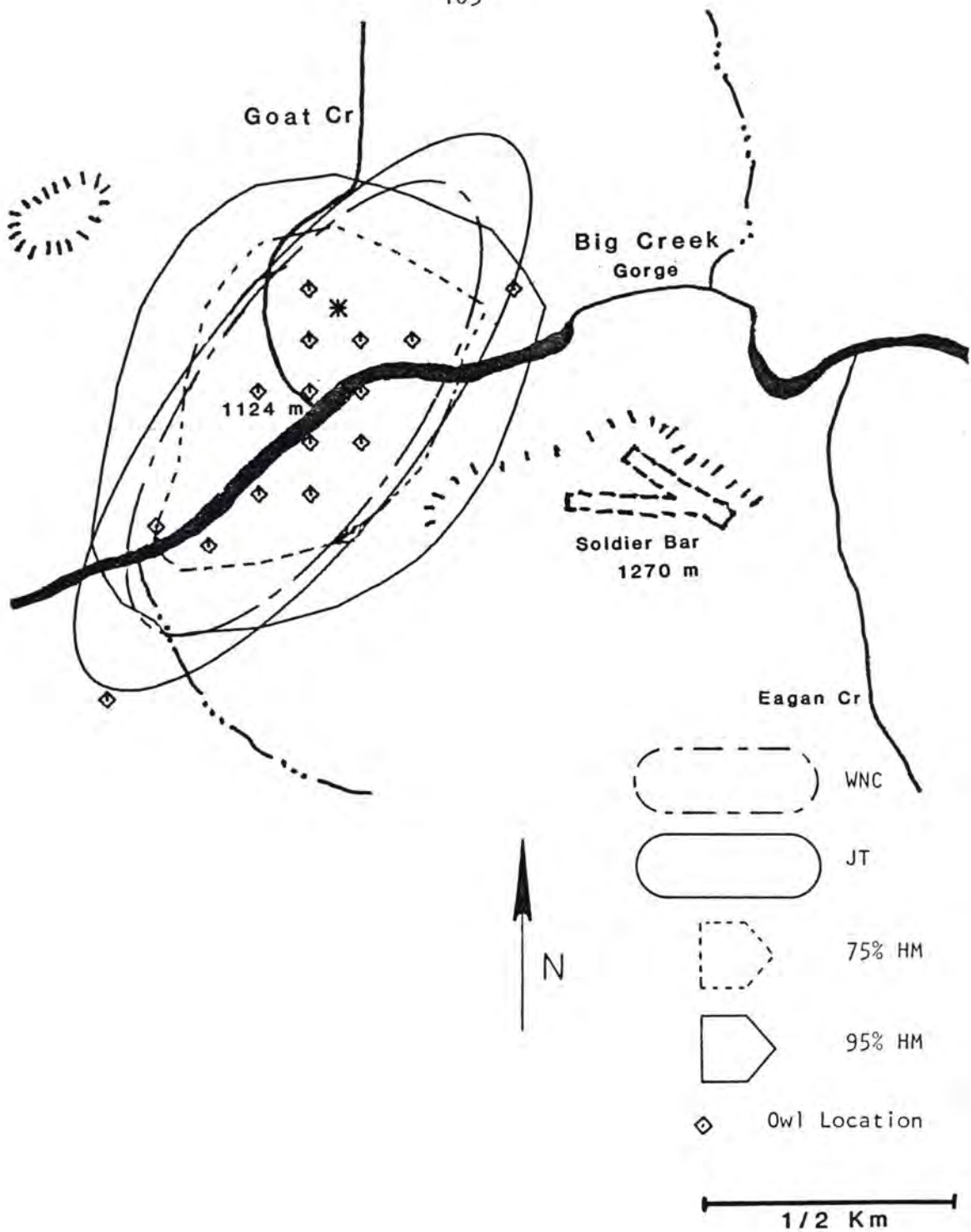


Fig. 15. Home range area of Screech - 25 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HM) using the program by Samuel et al. (1983).

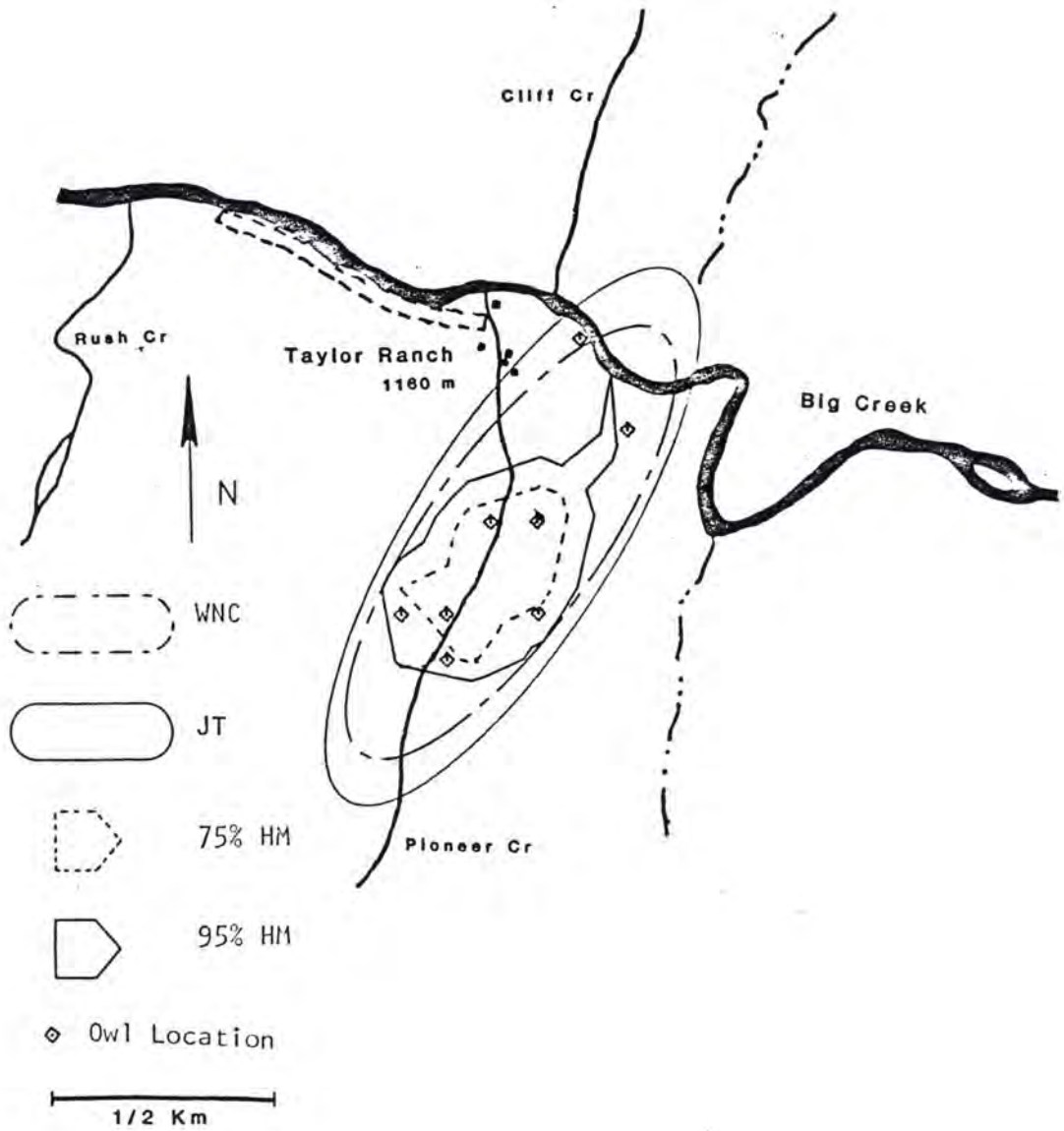


Fig. 16. Home range area of Saw-whet - 44 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% bivariate confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HM) using the program by Samuel et al. (1983).

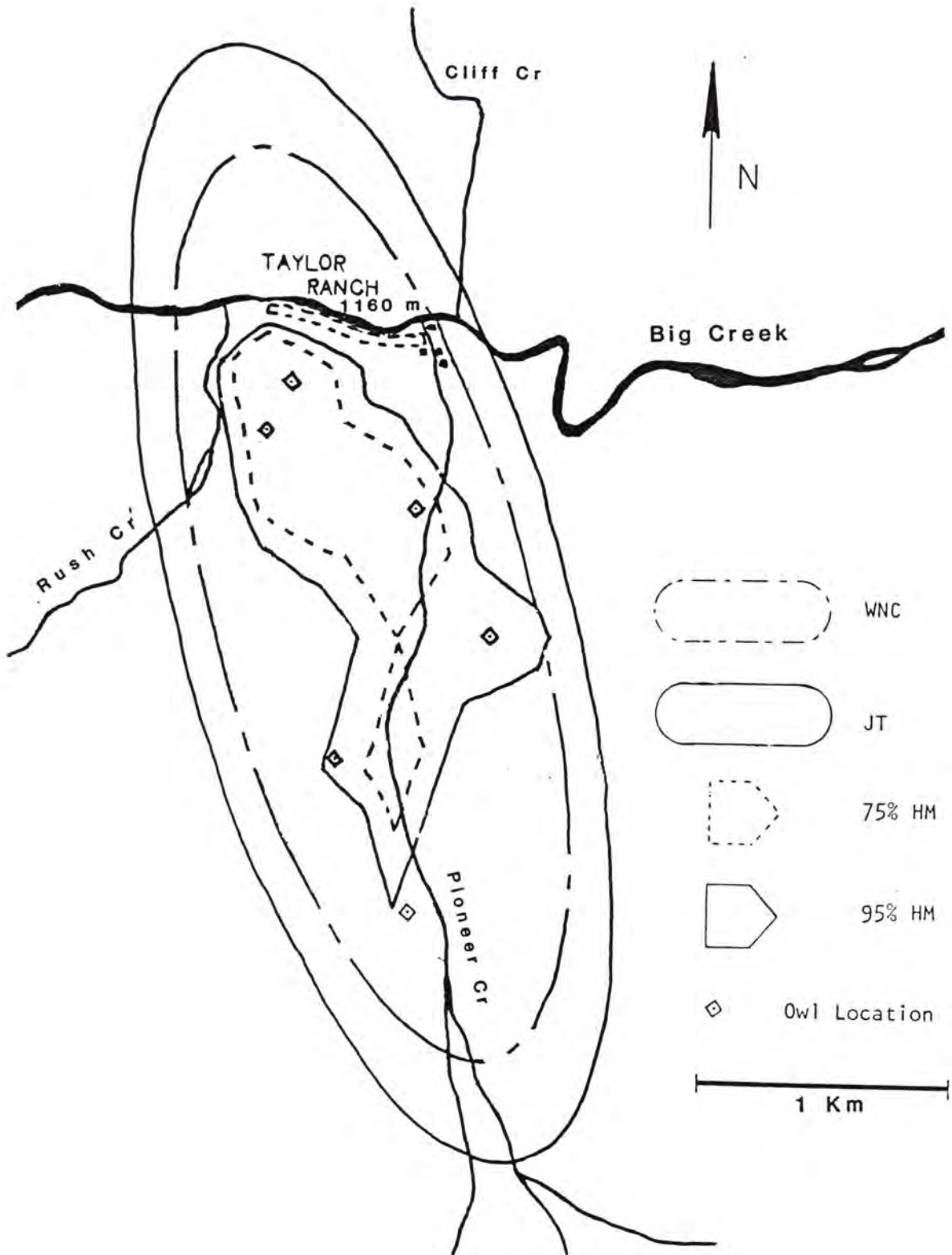


Fig. 17. Home range area of Saw-whet - 54 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% bivariate confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HM) using the program by Samuel et al. (1983).

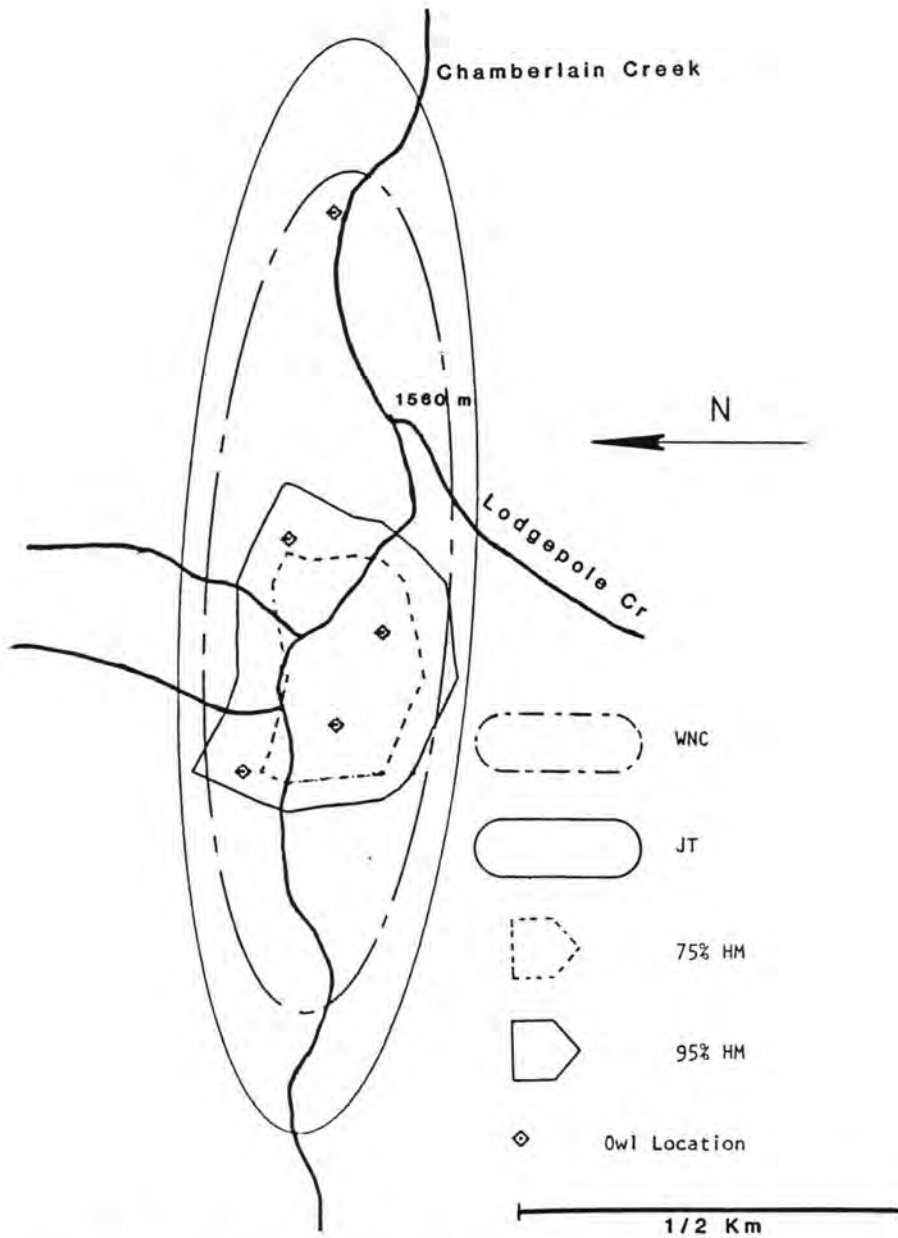


Fig. 18. Home range area of Saw-whet - 41 estimated using three methods: Weighted non-circular 95% confidence ellipse (WNC) (Samuel and Garton in review), Jennrich and Turner's (1969) 95% bivariate confidence ellipse (JT), and Dixon and Chapman's (1980) harmonic mean utilization volume (HM) using the program by Samuel et al. (1983).

saw-whet 54's home range included some areas used previously by saw-whet 44 who died before saw-whet 54 was captured.

Saw-whet 41 (Fig. 18), radio tracked from 12 March until 5 May

Although this owl was captured beneath a tree it had called from for over two hours the previous night it abandoned the area after being handled. The day after being captured it roosted 1.7 km from the capture site and moved 1.0 km (in the same direction) by 16 March. I did not radio track saw-whet 41 again until 4 April, and found the bird 2 km from the location of 16 March. Only those locations made after 16 March are used to estimate its home range area.

Comparisons With other studies

Forbes and Warner (1974) estimated a home range of 113 ha for a saw-whet owl radio tracked continuously for 20 days in early winter. Bondrup-Nielsen (1978:134) used only roost locations to estimate the home range of a saw-whet owl as 23 ha and of three boreal owls 500, 250, and 100 ha. These results and my own demonstrate variability in home range sizes of these three species. Abnormal short term movements by owls outside their home range will inflate our estimate of the area required by the bird, especially when nonstatistical estimates are used. Conversely, small sample size or a lack of foraging locations reduce the area estimates. Ideally home range analysis should

focus on delineating areas used intensively for foraging or roosting, rather than simply calculating the total area encompassed by the bird's movements. The structure of habitats in these 'core areas' can then be characterized as Nicholls and Warner (1972) have done with barred owls.

My estimates of home range area, provide preliminary data on the movements of owl species not previously studied in the western United States. The area estimates should be considered minimum home ranges for the period studied. The area intensively used by the owl is likely much smaller but larger samples are needed to define 'core areas'.

CHAPTER FOUR: MANAGEMENT IMPLICATIONS

Results of this study and inferences made therein must be considered with respect to the wilderness character of the study area and the limitations of the sample data. Very few boreal, screech, and pygmy owls were located. The sample, therefore, may not represent the normal range of variation in habitats selected by these species within the study area. Also, data on nest site selection and availability of nest structures were not gathered. Individuals were not observed while foraging so inferences concerning which habitats are most important to each species can not be made. Despite limitations of these data, I believe some comment on the management implications of this study is warranted. The data is most pertinent to central Idaho and any extrapolation outside this region must be done cautiously.

The wilderness character of the study site lends value to the study. This relatively unaltered forest ecosystem, provides an opportunity to study ecological relationships that may be obscured in the managed forest. Road building, logging, brush control, or other development may cause fluctuations in owl populations, which in turn would influence habitat selection (Partridge 1978). Human disturbance or man-made habitats may eliminate a species from otherwise suitable habitat or attract an inordinate number of individuals to an

area, confounding information on habitat preference. For example, gyr falcons have abandoned nest sites in response to harassment by aircraft (Platt 1977 according to Newton 1979), but raptors likely are attracted to artificially high prey populations near garbage dumps or grain storage.

In the wilderness setting, natural fluctuations in prey populations, effects of weather immediately prior to and during the study, and stochastic changes in owl populations on the study site will influence the data collected. Added variation due to human disturbance, is avoided, however. Therefore, habitat selection [and resource partitioning] should more closely reflect the innate habitat preferences of these resident owl species given the mixture of habitats available, competition present, and other environmental factors unique to the study sites. Knowledge of the species mix and habitat selection in wilderness will facilitate management of similar habitats outside wilderness.

Management on Non Wilderness Land

How many species of forest owls should a manager expect to find during a survey in the mountains of central Idaho? In the wilderness study area I found that three to five owl species commonly bred within any area 6 km in diameter. Great-horned and saw-whet owls likely breed throughout the mountains of Idaho except at the highest elevations. Other owl species will

be found locally depending on habitat.

Boreal and screech owls exhibit a limited elevational and habitat distribution and therefore warrant special attention. Screech owls inhabit riparian areas along major drainages with large cottonwoods. In areas without conifers, cavities in the cottonwoods are likely used for winter roosting as well as nesting. Long term management must protect existing large cottonwoods and assure their regeneration. Extremely heavy grazing may have a negative long term impact on screech owl populations by suppressing cottonwood recruitment and thereby eliminating future nest sites. Grazing will also affect the abundance, species composition, and availability of prey species. Moderate grazing may increase the availability of prey in riparian areas by removing cover. Heavy grazing, however, will reduce abundance of many prey species (Geier and Best 1980).

Boreal owl populations likely exist outside the RNRW in areas of the Canadian life zone. Broadcast call surveys for this species during February, March, and April will document their presence. Because few breeding populations of boreal owls are known south of Canada (Hayward in press), the effect of management activities on this species should be critically evaluated wherever boreal owls are located. In regions dominated by dense second-growth timber, open stands of overmature mixed conifers should be maintained for nesting, foraging, and roosting habitat. Single tree or group selection

management, or in some cases understory burning, can be used to promote an open old-growth stand structure and provide large old trees for future nesting snags.

Bondrup-Nielsen (1978) concluded that boreal owls in Canada selectively hunted meadow areas for meadow voles (Microtus pennsylvanicus), the major prey item. This species was never captured on trap grids under timber. My radio locations showed that boreal owls foraged along forest borders as well as in open old-growth timber. Clethrionomys gapperi, a mesic forest species (Gashwiler 1970, Ramirez 1977, Grant 1978), was the major prey species in the RNRW. This indicated that boreal owls were hunting the forest or forest border more intensely than inside the sagebrush shrub-fields. In Europe, Clethrionomys and Microtus are the major prey of Aegolius funereus (Fredga 1964, Norberg 1964, Sulkava and Sulkava 1971) again indicating they hunt forests or grassy meadows rather than shrub-fields. Forest management for boreal owls should favor wet meadows or grassy forest understory to encourage vole rather than mouse populations.

Logging operations should be concentrated in late summer and fall to avoid disturbing owls during courtship or nesting. Boreal owls are restricted to high elevations where timber values are lower and watershed and recreation values are high. Conflicts with wood production are therefore minimal.

The boreal owl uses artificial nest boxes in Europe (Norberg 1964) and Alaska (Meehan 1980). Providing artificial

nest boxes in habitats without suitable cavities (Common flicker or larger) may be one management alternative to maintain boreal owl populations. Forest plans which provide for scattered patches of oldgrowth timber would provide nesting snags.

Habitat requirements of saw-whet owls in this region appear compatible with most forest management activities. Deer mice (Peromyscus maniculatus), a major prey item in the RNRW and throughout the owl's range (Spurr 1952, Graber 1962, Collins 1963), are more abundant in clearcut forests of the northwest than in uncut stands (Gashwiler 1970, Ramirez 1977). The small, maneuverable saw-whet owl can also use moderately dense timber. Roosting occurs in trees from sapling to oldgrowth size. This owl, like the other small owls requires a nest cavity. Maintaining a sufficient density of snags over long periods may not be compatible with forest management which emphasizes timber production.

Throughout its geographic distribution the great-horned owl uses a wider variety of habitats than any other owl found in the RNRW. Therefore, management concerns will be less for this species than other owls. Management which creates an interspersed of openings in forest habitats and encourages snowshoe hare or cottontail (Sylvilagus) will favor great-horned owls. In some situations nest platforms may be limiting; here efforts to increase habitat suitability for diurnal raptors will also favor great-horned owls. In Canada,

Nero (1980) has encouraged great grey owls (Strix nebulosa) by building stick nests.

Although I observed only one flammulated owl in the RNRW, they likely breed throughout the wilderness area and much of southern Idaho. This species shows a strong preference for stands of overmature Ponderosa pine with two or more canopy layers (Marshall 1939, Bull 1978, Hayward, in review). This stand structure may be maintained by uneven-aged management, group selection, and controlled burns. Snags suitable for this secondary cavity nester must also be present. Because flammulated owls are migratory, logging from December until April, when the birds are gone, would avoid disturbance.

My understanding of pygmy and long-eared owl habitat preferences is too limited to suggest management. Pygmy owls nest in cavities, and long-eared owls on stick nests. Statements concerning nest sites for saw-whet and great-horned owls, respectively, apply to these species.

Management in the River of No Return Wilderness

Fire suppression and packstock in local areas significantly influence vegetation structure in the RNRW. Fire suppression reduces diversity and interspersed vegetation structure as successional communities are eliminated. Heavy grazing may change the species composition and abundance of small mammals in local areas by favoring deer mice and reducing

voles. In wet meadows this generalization may not hold true.

A fire management plan to allow wild-fires under certain conditions would maintain the natural diversity of vegetation structures in the RNRW. Scattered fire would create forest openings in some of the extensive tracts of lodgepole pine and Douglas fir timber. Owl species that hunt forest edges would be favored by the seral stages of succession. In some cases cool ground fire would stimulate understory vegetation and possibly increase small mammal populations.

Fire may be necessary to maintain the open, mixed conifer habitats used by boreal owls in the Chamberlain Basin area. Weaver (1974) stresses the importance of fire in maintaining open Ponderosa pine stands. Fire scars on many of the overmature Ponderosa pines on sites used by boreal owls at Chamberlain tell of past fires. Fire suppression will build fuel loads in these stands, and future fires under adverse conditions will be disastrous. Ponderosa pine, which provides the best nesting snags, will be eliminated in time because they occur in Douglas fir habitat types. Shading of the bole of Ponderosa pine and moisture stress in a dense stand makes the trees more susceptible to bark beetle infestation.

Finally, the U.S. Forest Service must be careful when cutting fuel-wood at Chamberlain Basin and Cold Meadows. Ponderosa pine and Douglas fir snags should not be cut. Loss of wildlife values through removal of old lodgepole snags for fuel-wood, however, is not a concern. Only live or recently

dead lodgepole pine are used for nesting by hairy woodpeckers, and northern or black-backed three-toed woodpeckers (Bull 1980).

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APPENDIX

Appendix 1. Summary of multiple stepwise discriminant analysis of three owl species at Taylor Ranch study site.

Characteristic	Canonical Discriminant Function	
	I	II
Eigenvalue	1.02	0.31
Chi-square test for significance of discriminant function	52	15
Degrees of freedom	12	5
Significance	< 0.001	0.013
Percent of discriminating information	77	23

Variable	Rotated Standardized Discriminant Function Coefficients	
	I	II
Deciduous cover above 8m (DEC)	1.071	-0.058
Bunch grass cover (BUNCH)	0.638	-0.461
Shrub cover 2-4m (SHRUBM)	-0.346	1.228
Number of plots without trees (MISSTREE)	-0.117	1.105
Shrub cover 1-2m (SHRUBS)	0.611	-0.781
Conifer cover above 8m (CON)	0.429	0.753

Classification matrix for three owl species at Taylor using the two canonical variates shown above.

Actual group	N	Predicted group membership		
		SW	SC	GH
Saw-whet	37	78% (29)	0% (0)	22% (8)
Screech	8	12% (1)	63% (5)	25% (2)
Great horned	14	29% (4)	0% (0)	71% (10)

Appendix 1. (continued)

Mean values for three owl species on two canonical variates.

Species	Canonical Discriminant Function	
	I	II
Saw-whet	-0.26	-0.54
Screech	2.20	1.09
Great horned	-0.57	0.80

Appendix 2. Summary of multiple stepwise discriminant analysis of three owl species at Chamberlain Basin study site.

Characteristic	Canonical Discriminant Function	
	I	II
Eigenvalue	2.15	1.04
Chi-square test for significance of discriminant function	36	14
Degrees of freedom	12	5
Significance	<0.001	0.02
Percent of discriminating information	67	33

Variable	Rotated Standardized Discriminant Function Coefficients	
	I	II
Forb ground cover (FORB)	1.321	0.148
Conifer cover 2-4m (CONM)	0.602	-0.032
Number of plots without trees (MISSTREE)	0.379	-0.209
Bunch grass cover (BUNCH)	0.083	0.947
Horizontal vegetation diversity (HDIV)	-0.191	-0.740
Conifer cover above 8m (CON)	-0.162	0.514

Classification matrix for three owl species at Chamberlain using the two canonical variates shown above.

Actual group	N	Predicted group membership		
		SW	B0	GH
Saw-whet	8	75% (6)	12% (1)	12% (1)
Boreal	8	0% (0)	100% (8)	0% (0)
Great horned	9	0% (0)	11% (1)	89% (8)

Appendix 2. (continued)

Mean values for three owl species on two canonical variates.

Species	Canonical Discriminant Function	
	I	II
Saw-whet	1.49	0.96
Boreal	-1.88	0.45
Great horned	0.34	-1.25
