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Author(s): G. D. Hayward and E. O. Garton
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Resource partitioning among forest owls in the River of No Return Wilderness, Idaho

G.D. Hayward and E.O. Garton
Department of Fishery and Wildlife Resources, University of Idaho, Moscow, ID 83843, USA

Summary. We studied resource partitioning among the forest owls in the River of No Return Wilderness, Idaho, during the winter and spring of 1980 and 1981. The owl assemblage consisted of five abundant species: pygmy (*Glaucidium gnoma*), saw-whet (*Aegolius acadicus*), boreal (*A. funereus*), western screech (*Otus kennicottii*), and great-horned (*Bubo virginianus*). Long-eared (*Asio otus*) and flammulated (*O. flammeolus*) owls were rarely observed. Information from the literature supplemented our data to describe the pattern of resource partitioning. Stepwise discriminant function analysis and multivariate analysis of variance revealed differences in macrohabitat and microhabitat. The saw-whet, boreal, western screech, and great-horned owls all preferred mammalian prey but exhibited habitat differences. They also differed in activity periods and food habits. 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 used areas within the territories of other owl species but specialized on forest insects. The observed pattern of resource use was interpreted to result from environmental factors, morphological limitations and interspecific competition. Differences in food and activity time, we suggest, result from environmental factors and differences in owl morphology, while present-day interspecific competition may be important in shaping habitat use. Experiments will be necessary to determine the causal factors responsible for segregation among the forest owls.

Key words: Forest owls – Competition – Habitat – Resources

Ecologists have long been interested in how species within a community partition available resources. Observational studies of resource partitioning encompass the full spectrum of life forms from plants (Werner and Platt 1976), marine and terrestrial invertebrates, to freshwater fishes, amphibians, reptiles, mammals, and birds (see reviews Schoener 1974, 1986; Toft 1985). Although early studies generally concentrated on resource partitioning among closely related organisms (see Schoener 1974), some recent work includes species assemblages involving diverse taxa defined by functional characteristics (Jaksic 1981; Belovsky 1984).

While early observational studies effectively described the pattern of resource use within communities, a considerable body of experimental work designed to discover the mechanisms responsible for those patterns has now accumulated (see reviews Connell 1975, 1983; Schoener 1983). Some argue that further observational studies hold little promise (Simberloff 1983; Strong 1983 among others). The trend toward manipulative experiments follows a call for an evolution in ecological investigation in which ecology shifts to a formal falsification of hypothesis approach (Simberloff 1983). This philosophy, however, is not held by all (Quinn and Dunham 1983; Roughgarden 1983 and others).

Despite the limitations of observational studies of resource partitioning, Schoener (1983) emphasized the importance of continued observational investigation. He noted that observational data can be gathered quickly to describe patterns in diverse environments and taxa. Interesting situations can then be selected for experiment. The two approaches complement one another.

Studies of resource partitioning within bird communities demonstrate the diversity of patterns in resource segregation. The resource dimensions recognized by Pianka (1978) have all been described as major axes for niche differentiation in various systems: space (Cody 1985a, 1985b; Terborgh and Weske 1975; Diamond 1973; Alatalo et al. 1985; Sherry and Holmes 1985; Noon 1981; Ford and Paton 1985; Brown and Bowers 1984; Wiens and Rotenberry 1981), food (Grant and Schluter 1984), and activity period (Ashmole 1965; but see Jaksic 1982). To address hypotheses concerning the degree and pattern of resource segregation and importance of competition 1) among trophic levels (Hairston et al. 1960), 2) among taxa, and 3) among environments (Wiens 1984a), data on resource partitioning from diverse communities will be required. Raptors, however, have received little attention (see Fuller 1979; Schmutz et al. 1980; Reynolds and Meslow 1984).

Due to the ease with which food data can be collected, ecological studies of owls have been particularly limited to studies of diet composition (see bibliography Clark et al. 1978). The evidence indicates owl populations are limited by food. In European boreal owls (*Aegolius funereus*) the influence of limited prey on population densities and movements has been demonstrated by Mysterud (1970) and Lundberg (1979). Southern (1970) and Hirons (1982) showed that food ultimately limits populations of tawny owls (*Strix aluco*) by affecting territory size and breeding success. Major works on resource partitioning among owls have described food niche differences in North America (Marti 1974) and Europe (Lack 1946; Herrara and Hiraldo 1976). In each case dietary overlap (especially size and life form of prey) was substantial.

Offprint requests to: E.O. Garton

Given the potential for food limitation but high dietary overlap, investigation of resource use in other niche dimensions is necessary to describe community structure. Southern and Lowe (1968) described the role of habitat in determining vulnerability of prey and ultimately the success of Tawny owl (*Strix aluco*) pairs. Lundberg (1980) examined food and habitat use by parapatric Ural (*Strix uralensis*) and tawny owls within a narrow zone of sympatry. He noted high food niche overlap but different habitat use and thereby demonstrated the shortcomings of a simple analysis of food habits.

Our objective here is to describe the pattern of resource use including habitat use, time of activity, and food, among the forest owls in the mountains of central Idaho. These owls constitute the entire nocturnal aerial predator guild that preys predominantly upon the small mammal populations of the forest and meadow ecosystems of this region. Drawing together our results and relevant literature, we describe a complex pattern of resource use among owl species in which differences in habitat use, food, and time of activity are all important.

Study area

The study was conducted in the 0.93 million hectare River of No Return Wilderness of central Idaho, U.S.A. Recent human impact in this roadless region has been limited to livestock grazing, trail systems and local disturbances associated with inholdings 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; Hornocker 1970). A study site was located in each portion.

The Taylor site was located in the rugged Big Creek canyon in the southern portion of the Wilderness. The site covered 49 km^2 and ranged in elevation from 1175 m (3855 ft) to 2195 m (7200 ft). The lower elevations were accessed from the University of Idaho Wilderness Research Center at Taylor Ranch; the higher elevations were accessed from a tent camp at Rush Point.

Douglas-fir--ninebark and Douglas-fir--pinegrass habitat types (Steele et al. 1981) dominate the moist aspects in both the Taylor Ranch and Rush Point vicinities. Drier aspects support bunch grass on the deeper soils and mountain shrubs on rocky soils. Relative proportions of vegetative cover types at Taylor, obtained from (1:15800) color aerial photos, were 49% Douglas fir (*Pseudotsuga menziesii*), 19% dry shrub, 17% bunch grass, 8% savanna, 3% rock, 2% deciduous bottom, and 2% other riparian. Douglas (1964), Hornocker (1970) and Claar (1973) describe the vegetation of the Wilderness Area in detail.

The Chamberlain Basin camp (43 km^2) represented a higher elevation life zone at 1722 m (5650 ft). Chamberlain Basin is dominated by even-age 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. A majority of the stands fall within the *Abies lasiocarpa* habitat type series. The relative proportions of vegetative cover types at Chamberlain were 36% open lodgepole, 32% dense lodgepole, 14% dense mixed conifer, 6% open mixed conifer, 4% riparian, 4% wet mountain grass, 2% dry shrub, and 2% bunch grass.

Methods

Locating owls

We broadcast tape-recorded owl calls nightly during the courting period 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 visited for 10-day periods on a rotating basis throughout the three-month census period. Survey routes were selected to allow sampling of all habitats and topographic positions at each study site. Foot or ski surveys were conducted in the evenings after dark and in the mornings before sun-up. We 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. Distant owls were approached for a more positive location. Boreal, saw-whet and screech owls captured in bal-chatri traps or mist nets (see references in Harris 1980) were radio-tagged using backpack or tail mounts. Radio marked owls were located on their diurnal roosts in order to collect pellets for prey analysis and to measure roost site characteristics which we reported elsewhere (Hayward and Garton 1984). A female boreal owl was located in her nest cavity through radio-tracking.

Vegetation sampling

Vegetation was sampled at singing, nesting and roosting locations in order to quantify microhabitat and macrohabitat characteristics of the forest used by the owls. Microhabitat here refers to vegetative conditions within a single relatively homogeneous stand of vegetation or such conditions at an ecotone where two vegetation types meet. Macrohabitat refers to characteristics of the environment in an area which likely will include the breeding season home range of one or more individuals. Macrohabitat, then, generally will include several vegetation types and landforms and is quantified by the proportion of the area covered by each.

The microhabitat at owl locations was sampled the following summer. Singing locations used in habitat analysis were all believed to represent different owls on separate territories. Cover of trees, shrubs and herbs was estimated on a macroplot established in homogeneous vegetation around the point location. Within the macroplot, eight 30.5 m parallel transects were established perpendicular to the slope. Transects were randomly spaced from 6 to 20 m apart. 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). We held a 2 m rod vertically as we walked the line transect to facilitate estimation of vegetation height and cover. We recorded the number of trees in five diameter classes (3–8 cm, 8–15 cm, 15–23 cm, 23–38 cm, and >38 cm) within two 100 m^2 (0.02 acre) circular plots per transect. Cover of forts, turf grasses and bunchgrasses was recorded separately on five 0.1 m^2 rectangular plots (Daubenmire 1959) systematically located along each transect. We 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 (Appendix 1). Mean tree density was calculated using only those plots which had

trees. The frequency of nontimbered plots within the macroplot was also recorded.

Macrohabitat vegetation was sampled by classifying vegetation on color aerial photos (1:15800) into eight categories on the basis of dominant vegetation cover. Using a planimeter we measured the percent cover for each vegetation category at both study sites using the area within 0.8 km of all survey routes to define the study area boundary.

We measured macrohabitat at singing locations by circumscribing a circle about each location plotted on aerial photos. These circles enclosed an area representative of the owl's home range. We incorporated information from Craighead and Craighead (1956), Forbes and Warner (1974) and our own unpublished data to define the standard home range radius for each species (pygmy owl – 0.5 km, saw-whet owl – 0.5 km, boreal owl – 0.7 km, great-horned – 1.0 km). We used a planimeter to measure the proportions of each vegetation cover category occurring within each "owl home range".

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, we used a 1260 by 480 m rectangle with semicircular ends on the long axis, oriented along the stream's course.

Food habits

Prey species were identified from regurgitated pellets collected beneath roost sites (and in a single boreal owl nest) which were located by radio-tracking. 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, we 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 compliance with this assumption. Percentage data received arcsine square root transformation and timber densities the square root transformation (Johnson and Wichern 1982).

To find a subset of compound variables which would maximize the microhabitat differences between four owl species, a matrix of twenty-five vegetation variables for each of 84 observations was entered into stepwise canonical discriminant analysis (Klecka 1975). Values were first standardized to z-scores to eliminate distortions which result from variously scaled data (Aspey and Blankenship 1977).

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, 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). Our data, like most resource use data, violated this assumption as indicated by rejection of the null hypothesis, using Box's M statistic ($P<<0.01$) (Klecka 1975). Harris (1975), however, 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 to judge their significance by their ecological interpretability and by 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.

To compare the vegetation cover within owl home ranges to that available at the stuy site (macrohabitat selection) we used Hotelling's T^2 test (Johnson and Wichern 1982). Individual t-values with an absolute value greater than the tabled-t indicate specific vegetation types were selectively used (+) or avoided (−) by the species. A significant F statistic for Hotelling's T^2 will protect the error probability, permitting multiple comparisons using several t-tests. Differences in macrohabitat selection among the owl species were identified by multivariate analysis of variance. Univariate ANOVA and significant difference multiple comparisons indicate which vegetation types were used most differently by the owl species (Ott 1977).

Macrohabitat specialization was further explored by examining niche breadth. Using Feinsinger et al.'s (1981) method, niche breadth was defined as the degree of intersection between the frequency distribution of available cover types and those found in the owl home range. The home range, as described earlier, is a standard circle around owl locations.

Results

We observed seven breeding owl species 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 (*A. 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, western screech owls (*O. kennicottii,* hereafter screech owl), pygmy owls, and long-eared owls (*Asio otus*) were heard to a lesser extent. Four saw-whet owls, three screech owls, and one boreal owl were radio-tagged.

Habitat selection

We used the location of calling owls as an indication of habitat use. We are confident 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. It is generally believed that singing locations represent potential breeding sites (Bondrup-Nielsen 1978).

Macrohabitat: We found significant differences between habitats used by owls and those available to them (Table 1). 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 must be interpreted with caution for the great-horned and saw-whet owls at Chamberlain, and the pygmy owl at both study sites because of the insignificant T^2 for these comparisons.

Table 1. 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. 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 t-values are shown ($P<0.05$)

		Species				
Site	Habitat/Statistic	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
	N	8	8		22	5
	Tabled-t (=0.05)	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	
	N	5		9	9	2
	Tabled-t (=0.05)	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	

Great-horned, boreal and saw-whet owls did not differ significantly in macrohabitat use at Chamberlain (Multivariate ANOVA, Wilk's Criterion $P=0.108$). 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 2). Disproportionate use of deciduous bottoms by screech owls was the most significant macrohabitat difference among these owls. Screech owl home ranges also included a higher proportion of bunchgrass habitat than did other owl home ranges. This difference is expected since bunchgrass habitats were often adjacent to river bottoms on southern exposures.

Screech owls had the most narrow macrohabitat niche breadth, restricting activity to deciduous habitat in the lowest elevations at Taylor (screech = 0.128, saw-whet = 0.318, great-horned = 0.455). At Chamberlain, boreal and great-horned owls showed wide niche breadths (saw-whet = 0.158, boreal = 0.315, great-horned = 0.341). The saw-whet owl reduced its niche breadth between Taylor and Chamberlain where the congener boreal owl was the most common owl.

Microhabitat: We used multiple stepwise discriminant analysis to identify structural features of the vegetation which were most different between singing locations of four owl species. In preliminary analysis, pygmy owl habitat could not be distinguished from other species as indicated by extremely low classification success. This species was using a broad range of habitats which overlapped with all the other species. The pygmy owl, therefore, was removed from calculation of the functions so that it would not overly influence the derived canonical variates. Three canonical variates derived from ten habitat variables were judged significant by a chi-square test and retained for interpretation of owl habitat preferences (Table 3).

Screech owls and boreal owls differed along a gradient of deciduous cover in the 4–8 m height class (canonical variate I, Fig. 1). The screech owl occurred in riparian areas with abundant deciduous cover at this height while boreal owl habitats had few tall shrubs. The second axis represented a gradient of shrub cover and habitat patchiness (canonical variate II). 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 used habitats with open shrub patches (positive end of the gradient; Fig. 1). The third axis identified coniferous cover at various heights. Boreal owls used coniferous stands having well-developed low and high canopy but lacking a mid-canopy layer. Saw-whet owls used habitats representing the average of all three gradients but favored non-deciduous forest stands with a well-developed mid-canopy layer and shrubs in the 1–2 m height class.

Figure 2 shows the degree of overlap between species on the three most discriminating microhabitat variables. Saw-whet, screech, and boreal owl microhabitat structures overlapped little. The saw-whet owl shows little variability on axes I and III indicating a narrow range of habitat selec-

Table 2. Multivariate analysis of variance testing differences in macrohabitat selected by four owl species at Taylor. Least significant difference tests are used for multiple comparisons. Under-scored species are not significantly different ($P \leq 0.05$). GH = Great Horned owl ($N = 8$), SC = Screech owl ($N = 8$), SW = Saw-whet own ($N = 22$), PY = Pygmy owl ($N = 5$)

Habitat	F	Prob. $>F$	Multiple comparison			
Douglas fir	1.27	0.298	GH	SC	SW	PY
Bunch grass	2.48	0.075	SC	PY	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	SC	GH	SW	PY
Rock	2.18	0.106	GH	SC	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

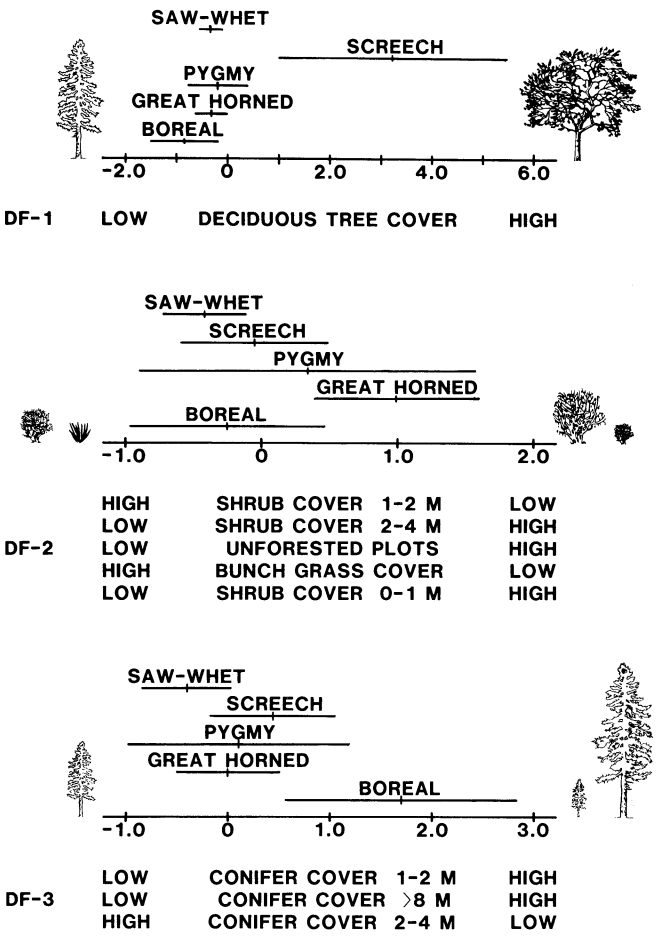

Fig. 1. Mean and 95% confidence intervals for the positions of 5 owl species along 3 independent microhabitat dimensions chosen by discriminant analysis

tion for non-deciduous stands (variate I) and even-aged, single layered conifer habitats (variate III). Boreal and 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 (Noon 1981). Over two thirds of the observations were correctly classified. All misclassified boreal owls were classified as saw-whet owls, the boreal owl's congener (Table 3). The smaller saw-whet owl was rarely misclassified as a boreal owl. No owls were misclassified as screech owls, although saw-whet and great-horned owls sometimes occupied territories adjacent to screech owls along Big Creek.

Microhabitat segregation along three habitat gradients is apparent when 95 percent confidence intervals for species' centroids are examined (Noon 1981, Fig. 1). 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, pygmy/great-horned and pygmy/saw-whet. Results of separate canonical discriminant analysis calculated for both study sites and R-factor analysis of the microhabitat data support these trends (Hayward 1983).

Finally, we measured niche overlap using three canonical discriminant functions as niche dimensions (Appendix 2). Our procedure used an extension of the two-dimensional measure of overlap using 95% confidence ellipses presented by Dueser and Shugart (1979). Here, however, we employed the program MONTECAR (Kintner 1987)

Table 3. Summary of multiple stepwise discriminant analysis of microhabitat utilized by 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	<0.001	<0.001	0.004
Percent of discriminating information	61	22	17

Variable	Rotated standardized discriminant function coefficients I	II	III
Deciduous cover above 8 m (DEC)	0.984	−0.187	0.107
Aspen density (ASPEN)	−0.442	−0.229	0.228
Shrub cover 1–2 m (SHRUBS)	0.334	−1.548	−0.293
Shrub cover 2–4 m (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 0–1 m (SHRUBL)	−0.203	0.717	−0.395
Conifer cover 1–2 m (CONS)	0.089	0.321	1.030
Conifer cover above 8 m (CON)	0.422	0.173	0.681
Conifer cover 2–4 m (CONM)	−0.160	−0.009	−0.435

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%

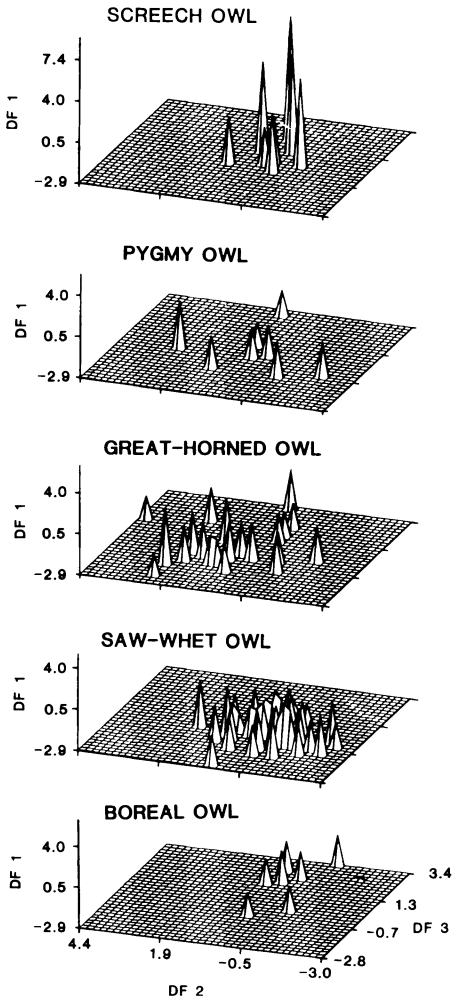

Fig. 2. Distribution of 5 owl species along 3 microhabitat resource dimensions. Each dimension represents a discriminant function significant in separating at least one pair of owl species. See Fig. 1 for habitat characteristics represented by each axis

which incorporates the concept that species' realized niches include optimal and suboptimal regions which can be modeled as multivariate normal distributions. Overlap, then, was treated in a prohabalistic sense such that overlap was not simply the volume of intersection for two species' multidiemensional niches but a probability distribution within realized niches (Kintner 1987). The pattern of niche overlap between these owls supports the results of analysis presented above (Appendix 2). Screech owls overlap the other species very little. Niches of the generalist pygmy and great-horned owls encompass large portions of the niches of the other species.

Temporal activity

Radio-tagged boreal, saw-whet and screech owls all began foraging each evening within 45 min of sunset (Hayward 1983). The circadian activity of a boreal owl was closely monitored for 12 days during the nesting period using an automatic event recorder attached to the nest cavity. The time of prey deliveries indicated a highly nocturnal, biphasic activity pattern; 83% of all records occurred between 2100 and 0600. Activity peaked at 2200 and 0400 with a significant lull at 0200 (Hayward 1983). On four occasions radio-marked saw-whet owls were observed leaving their daytime roosts from 0 to 22 min after sunset. Departure times for radio-marked screech owls ranged from 12 min before to 27 min after sunset in the seven observed cases.

Food selection

Eleven prey species were identified from pellets found beneath roosts and in the nest cavities of great-horned, saw-whet, screech and boreal owls (Table 4). An insignificant 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 ($P=0.085$, df$=8$, $X^2=13.89$, Table 5). A high proportion of shrews (2–15 g) occurred in the saw-whet owl diet, whereas few shrews were taken by boreal owls which took large numbers of red-backed voles (*Clethrionomys gapperi*) (cell chi-square significant for saw-whet owl prey less than 15 g, $P<0.05$). This difference contributed most to chi-square value. Small rodents 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

Table 4. Prey identified in pellets of four owl species in the River of No Return Wilderness, Idaho. Weights are from Burt (B:1952) and unpublished data from the study area (U)

Prey	Weight (grams)	Number of prey			
		Saw-whet	Boreal	Screech	Great-horned
Mammal					
Sorex spp.	4 (U)	4	1	2	
Sorex vagrans	4 (U)	1			
Peromyscus maniculatus	24 (U)	8	9	4	1
Clethrionomys gapperi	27 (U)	1	35		
Phenacomys intermedius	23 (U)	1	5		
Microtus longicaudus	30 (U)	2			
Microtus spp.	30 (U)		1		
Microtus montanus	30 (U)		1		
Glaucomys sabrinus (juv.)	est. 50 (U)		1		
Thomomys talpoides	103 (B)		2		
Neotoma cinerea	300 (U)			1	2
Sylvilagus nuttalli	800 (B)				1
Unknown mammal		7	11	7	1
Birds					
Unknown bird		1	9	2	
Bubo virginianus					1

Table 5. Comparison of types and size classes of prey in pellets of three owls in the River of No Return Wilderness, Idaho. Sample sizes exceed those in Table 4. Long bones from pellets without skulls (and therefore without good evidence of prey species) were compared to known specimens and placed in size classes

Prey type	Size class	Number of prey for each owl species		
		Saw-whet	Boreal	Screech
Mammal	2–15 g	6[a]	2	2
	16–35 g	18	61	11
	36–60 g	0	1	0
	>60 g	0	2	1
Bird		1	9	2

[a] Cell x^2 significant ($P<0.05$)

in spring (Graber 1962); boreal owls concentrate on *Microtus* and *Clethrionomys* (Norberg 1964; Sulkava and Sulkava 1971; Bondrup-Nielsen 1978) in Europe, 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); pygmy owls take small mammals, birds and insects in almost equal proportions (Earhart and Johnson 1970); and flammulated owls are insectivorous (Marshall 1939; Hayward 1986). 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

Niche pattern

In contrast with other studies of owls, we sought to describe resource use by all forest owl species occurring within a restricted but diverse geographic region. Our results indicate the owls differ in habitat, food, and time of activity in a complex manner. Most striking, in light of other analyses which have concentrated on food resources (Lack 1946; Marti 1974; Herrerra and Hiraldo 1976; Jaksic 1983), is the pattern in habitat use shown by these owls. The only species pairs without habitat differences were those involving pygmy owls.

Of the five most abundant species, the two most similar in size, boreal and screech owls, differ in macrohabitat through non-overlapping elevational distributions. Macrohabitat utilization by sympatric owls was statistically different only at Taylor where screech owls used deciduous types more than other owls. Even in this case, however, species' distributions overlapped substantially. Individual screech, great-horned, and saw-whet owls used river bottom habitats. This overlap in habitat among screech, great-horned and saw-whet owls in the riparian zone is further indicated in microhabitat analysis. Three screech owl calling sites were misclassified as saw-whet or great-horned in discriminant analysis. On the other hand, great horned and saw-whet use areas were never misclassified as screech owl. Possibly saw-whet and great-horned owls inhabit only river bottom habitats which provide vegetation structures similar to areas used outside the river bottom. The screech owl, however, may be capable of using all the river bottom habitats. The important differences in deciduous cover between screech owls and the other species is apparent in the first discriminant axis (Table 3). Saw-whet/boreal, saw-whet/great-horned and boreal/great-horned species pairs also differed in structural characteristics of microhabitats used.

Pygmy owls exhibited broad habitat association. The species occurred at both Chamberlain and Taylor and seemed to be most associated with open, large diameter conifer stands but showed substantial variation in habitat use. Overlap in microhabitat between the pygmy owl and other species was substantial.

Although pygmy owls differed little from other species in habitat use (niche overlap measured on all three discri-

minant axes for microhabitat were greater than 70% with boreal, saw-whet and great-horned owls, Appendix 2), it is the most diurnal species of the owl assemblage (Bent 1961). Foraging during daylight, pygmy owls capture a higher proportion of birds than the other owls and, in general, consume a wide range of prey (Brooks 1930; Earheart and Johnson 1970). The European pygmy owl (*Glaucidium passerinum*) has poor night vision (Mikkola 1983, p. 116) but we found no data for *G. gnoma*. Available information on the other forest owls and data we gathered indicated primarily nocturnal activity (references earlier). Studies by Graber (1962) on saw-whet owls, Klaus et al. (1975) on the boreal owl and Hayward (1986) on flammulated owls show these species exhibit a biphasic circadian rythmn with activity peaks at nightfall and again just before dawn. Norberg (1964) found boreal owls first visiting their nest 40–60 min following sunset. VanCamp and Henny (1975) felt screech owls were highly nocturnal, and Allen (1924) noted prey deliveries to a nest throughout the night. These studies support our observations that activity begins at dark and ends at dawn for boreal, saw-whet and screech owls. Few other investigations have specifically measured the circadian rythmn of forest owls. In northern Idaho, Frounfelker (1977) observed radio-tagged great-horned owls beginning activity at sunset. In Colorado great-horned owls began hunting before complete darkness, departure averaging 20 min after sunset (Marti 1974). The pygmy owl is generally characterized as hunting mostly during daylight hours (Sprunt 1955; Eckert and Karalus 1974).

Differences in food habits among the three medium-sized owls – saw-whet, boreal and screech – were minor. Niche overlap in size class of prey taken by these three owls exceeded 67% and sympatric saw-whet and screech owls overlapped 85% (niche overlap using Schoener's (1970) measure: saw-whet/boreal 72%; saw-whet/screech 85%; boreal/screech 67%). In southern Wisconsin, where saw-whet, screech and great-horned owls are sympatric, food niche overlap calculated by Jaksic (1983, from data of Errington 1932) were all over 62%.

The species composition of owl prey, on the other hand, differed substantially. Any differences in prey species, however, cannot be taken to necessarily indicate selective preference for different prey. Subtle differences in diet are as likely a consequence of differing foraging habitats among the owl predators as is selection for particular prey species. Foraging theory would suggest that, within a habitat patch, if two prey species are encountered, each of similar size and similar defense capabilities, both prey types should be consumed (Orians 1971). Schoener (1986) notes that food specialization is less likely than habitat specialization because time and energy are lost in moving from patch to patch for the specialized food. In our studies, saw-whet, boreal and screech owls each consumed more prey in the 16–35 g size class than any other size, indicating they are each quite capable of killing prey in this size range. Boreal and saw-whet owls consumed deer mice and red-backed voles in different proportions. These two small mammals generally prefer different habitats (unpublished data). It seems reasonable, then, to interpret the difference in consumption of deer mice by saw-whet and boreal owls as a consequence of selection by the owls for habitat rather than prey species. Others who have not studied habitat associations of owls have interpreted differences in owl diets to indicate prey selection (e.g., Marti 1974; Herrera and Hiraldo 1976; Jaksic 1983). Considering the habitat associations of both prey and predator, an argument for habitat selection seems equally satisfying. Experiments testing for preferences by owls for particular prey species will be necessary to solve the debate.

Although we collected little data on resource use by flammulated and long-eared owls, these species should be considered in a discussion of resource use within the owl assemblage. In 1985, during intensive studies of boreal owls, four flammulated owl territories were located at Chamberlain and a long-eared owl was observed.

Flammulated owl singing sites have all been within 100 m of known boreal owls nests indicating substantial overlap in habitat use. 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, flammulated owls are strictly insectivorous, feeding mainly on nocturnal moths (Marschall 1939; Johnson and Russell 1962; Hayward 1986).

We have no data on habitat associations of long-eared owls in our forest habitats. Food habits and activity time, however, have been well documented in other regions. The species can be characterized as a nocturnal predator of small mammals under 100 g (Marks and Yensen 1980) with 89% of its prey between 20 and 50 g in a Colorado population (Marti 1974). Prey of long-eared owls, then, differs little in size and life form from the medium-sized owls in the assemblage, and the species forage at the same time of day.

Community structure

What does this pattern of resource use indicate about community structure? Even species existing without strong interactions should be expected to differ from one another; a randomly contrived community will have species that show differences (Schoener 1986). Is there any evidence that resource use in the owl assemblage results from species interactions, or can the resource use pattern be explained more parsimoniously as the independent reactions of each species to the environment (for example Jarvinen and Haila 1984; James and Boeklen 1984)? If species interactions are important, which classes of interactions likely contribute most to the structure?

As demonstrated by Toft (1985) for amphibians and reptiles, a number of factors including physiological and morphological constraints, predation, and competition contribute to structure in resource partitioning. We wish to determine the contribution of each factor in determining the structure of the owl community (Quinn and Dunham 1983). Because our information is limited to observation, however, the techniques used so elegantly by Dunham (1980) and Poysa (1983) are not suitable. Rather, we will compare the pattern of resource differences among the owls using several criteria developed below.

If resource use among each species of owl is independent of other owl species due to physiological or morphological constraints or to specialized adaptations to particular environmental characteristics (Wiens 1984b), we should expect: 1) all species to be clustered at resource optima, or 2) species to have randomly spaced resource use distributions. A random pattern would result, for example, if various species developed independently in an environment with a broad

Table 6. Resource dimensions most different in the niches of five forest owls. The resources are symbolized as follows: Ma = Macrohabitat, Mi = Microhabitat, T = Time of activity and F = Food

	Pygmy	Saw-whet	Boreal	Screech	Great-horned
Flammulated	FT	F	F	FMa	F
Pygmy		FT	FT	FT	FT
Saw-whet			Mi	Mi	FMi
Boreal				Ma	FMi
Screech					FMi

range of resource availabilities. If predation, parasatism or other non-competitive biotic interactions have significantly influenced the owl community, we expect populations of one or more owls to be held below levels where resources limit population size. Strong (1984) describes this situation for phytophagous insects controlled by parasitoids. Also, resource use should not shift due to the presence or absence of another owl species unless that owl is a predator or competitor.

If population characteristics and resource use do not fit the above patterns, competition may be influencing the community. Schoener (1974, 1986) describes several criteria which implicate competition in structuring resource use patterns. Competition should result in overdispersed niches recognized by: 1) regular spacing of resource use along a single resource dimension, 2) an increase in the number of important dimensions as the number of species increase, and 3) the separation of species along complementary dimensions.

What factors structure the resource use pattern?

For the group of owls studied, segregation is not apparent between all owl pairs on any single resource axis. The overall pattern of resource use is not random, however, and appears to show structure at several levels. The largest and smallest owls differed from all others most in food, whereas intermediate-sized owls differed from one another most in habitat use (Table 6). What factors might contribute to segregation in food and habitat?

Although pygmy owls do capture mice and voles, prey weighing 90% of their own weight are likely not optimum. Instead they concentrate on small birds and insects. The larger size and greater strength of great-horned owls permits the capture of large prey. Morphological considerations rather than species interactions can explain the differences in food among these species. The three medium-sized owl species (saw-whet, boreal, and screech owls), on the other hand, all consume small mammal prey in a narrow size range (16–35 g), such that resource use is clumped at a single optimum. This pattern of food use is suprising considering the range in size of these owls (80–232 g, unpublished data). Again, the simplest explanation for this observation is the high productivity of small mammal prey in this size class and constraints on foraging methods due to owl morphology. Adaptations for nocturnal forest foraging – relatively slow, silent flight, sit-and-wait hunting behavior, and visual and auditory capacities to detect small, nocturnal, terrestrial prey – predispose these owls to hunting small mammals (Mikkola 1983).

The three owl species whose food niches are most similar differ most in habitat use. Significant differences in microhabitat use (Fig. 1) suggests overdispersion on this niche dimension. These differences in habitat could be a consequence of 1) predation forcing species into habitat refugia (Werner 1984, pp. 378), 2) morphology limiting the range of habitats which a species may use, or 3) competitive interactions forcing species into particular habitats (example Werner 1984). Although predation on owls by other hawks and owls has been well documented (references in Herrera and Hiraldo 1976), we have seen no evidence for population regulation through predation. In well-studied populations, predation has not been an important regulating factor (Southern 1970; VanCamp and Henny 1975). Morphology, per se, should not completely limit habitat use by these owls, as all are forest species. Werner (1984), however, has shown that the interaction of morphological features and exploitative competition can determine habitat choice in sunfish. We suggest, then, that according to Schoener's (1974) criteria (niche complementarity seen in Table 6, and overdispersion in habitat use), the pattern of habitat segregation suggests competition may be important in structuring habitat use within the owl assemblage, assuming food resources are limiting (Wiens 1977, 1984a). Our studies subsequent to this investigation do indicate that small mammal populations decline to very low densities in some years and that boreal owl breeding activity is limited by prey availability at Chamberlain (unpublished data).

Mechanism for habitat segregation

In the preceding section we argued that the pattern of habitat use suggested interspecific competition as a major structuring force. What mechanisms could facilitate effective segregation by habitat to reduce competition for food among the small mammal specialists? All of these species are similar in morphology, possessing the classic owl features described by Mikkola (1983). All are forest owls, and lists of prey indicate they hunt forest habitats. Like Werner's (1984) sunfish, when prey is abundant habitat use could be expected to be similar – all owls taking advantage of prey wherever it is most available. As prey availability decreases, however, slight differences in morphology could permit species to exploit different habitats more efficiently (Schoener 1982). Hespenheide (1973, 1975) argued that competing species should adjust niche widths by restricting or changing 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. This would suggest that, in owls, differences in the structure of wings, eyes and ears rather than feet would reveal the important differences permitting optimal foraging under different circumstances. For instance, species with more acute and directional hearing would be more effective hunting prey concealed by snow or a grass mat, whereas more acute nocturnal vision would allow flight through dark forest canopy. Whether these species rely on hearing or vision to different degrees is not known. These data and information on foraging behavior would be quite valuable.

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,

Table 7. Variation in wing structure of seven owl species. Wing loading is calculated from wing area (cm^2) divided by bird weight (g). Wing length index is calculated from wing chord (cm) divided by the cube root of bird weight (g)

Owl species	Wing loading ($cm^2 g^{-1}$)	Wing length index ($cm\ g^{-1/3}$)	Source
Saw-whet	3.88		Poole (1938)
	3.49	3.27	This study $N=4$
		3.12	Snyder & Wiley (1976)
Screech	1.87		Poole (1938)
	2.27	3.02	This study $N=2$
		2.97	Snyder & Wiley (1976)
Long-eared	5.13		Poole (1938)
	4.22		Poole (1938)
		4.42	Snyder & Wiley (1976)
Great-horned	1.77		Poole (1938)
	1.64		Poole (1938)
		3.18	Snyder & Wiley (1976)
Pygmy		2.29	Snyder & Wiley (1976)
Boreal		3.41	Snyder & Wiley (1976)
	2.51	3.24	This study $N=2$
Flammulated		3.44	Snyder & Wiley (1976)

while relatively larger wing areas lower the flight speed. The long-eared owl has a light wing loading and a long wing (Table 7), features consistent with hunting 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 our information indicate the saw-whet owl hunts in denser forest cover than sceech or boreal owls. Added maneuverability is, therefore, required. The lighter wing loading may also be better suited for transporting relatively larger prey. These differences in wing structure combined with differences in the owls' size could represent differences permitting the owls to hunt habitats of various structure more efficiently.

Implications

The complex pattern of resource partitioning among forest owls in central Idaho can be explained only as the result of several factors. We suggest that environmental character-

Appendix 2

Three dimensional niche overlap computed from a probabalistic model assuming multivariate normal niches defined by factor scores from canonical discriminant analysis (Kinter 1987). The table displays the probability that the habitat niche of a member of species A is found in the habitat niche of species B

	Species B				
Species A	Pygmy	Saw-whet	Boreal	Screech	Great-horned
Pygmy		0.686	0.606	0.256	0.956
Saw-whet	0.978		0.584	0.438	0.968
Boreal	0.712	0.430		0.064	0.800
Screech	0.176	0.160	0.112		0.266
Great-horned	0.714	0.530	0.482	0.232	

Appendix 1

Vegetation structure variables measured within macroplots 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	Mean of eight line intercept transects
SHRUBM	Percent deciduous shrub cover 2–4 m high	Mean of eight line intercept transects
SHRUBT	Percent deciduous shrub cover 4–8 m high	Mean of eight line intercept transects
CONL	Percent conifer cover 0–1 m high	Mean of eight line intercept transects
CONS	Percent conifer cover 1–2 m high	Mean of eight line intercept transects
CONM	Percent conifer cover 2–4 m high	Mean of eight line intercept transects
CONT	Percent conifer cover 4–8 m high	Mean of eight line intercept transects
CON	Percent conifer cover 8 m high	Mean of eight line intercept transects
DECT	Percent deciduous tree cover 4–8 m high	Mean of eight line intercept transects
DEC	Percent deciduous tree cover 8 m high	Mean of eight line intercept transects
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	Mean of 40, 1/10 m^2 rectangular plots
FORB	Percent cover of forbs	Mean of 40, 1/10 m^2 rectangular plots
MALL	Percent total herbaceous cover	Mean of 40, 1/10 m^2 rectangular plots
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	Mean of 16, 0.02 acre circular plots
POLE	Number of trees 6–9 in DBH	Mean of 16, 0.02 acre circular plots
MATURE	Number of trees 9–15 in DBH	Mean of 16, 0.02 acre circular plots
OLD	Number of trees 15 in DBH	Mean of 16, 0.02 acre circular plots
ASPEN	Number of aspen trees	Mean of 16, 0.02 acre circular plots

istics, constraints on morphological and behavioral adaptations and interspecific competition all influence the pattern of use of space, food and time. These factors interact and all contribute to the observed resource use pattern. We have sought to determine the relative contribution of these factors in determining resource use. Past work has generally emphasized the importance of dietary segregation among owls. Our results suggest that differences in habitat use by forest owls may be an important aspect of community structure. Unfortunately field experiments with such low density, wide ranging birds have not been performed because of the obvious difficulty, but they may not be impossible. Nest box studies in Scandinavia (eg. Lofgren et al. 1986) have shown that populations of boreal owls can be manipulated. By measuring resource abundance, resource use, and owl densities (for the entire forest owl guild) during such manipulations, considerable insight into community structure could be gained. By altering habitat structure through logging and concurrently monitoring owl species abundance, a test of the habitat segregation model may be possible. Finally, investigation of foraging habitat use by owls in conjunction with studies of resource availability and use also holds promise.

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