COMPARATIVE HABITAT USE OF SYMPATRIC MEXICAN SPOTTED AND GREAT HORNED OWLS

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Abstract: To provide information on comparative habitat use, we studied radiotagged Mexican spotted owls (*Strix occidentalis lucida*: $n = 13$) and great horned owls (*Bubo virginianus*; $n = 4$) in northern Arizona. Home-range size (95% adaptive kernel estimate) did not differ significantly between species during either the breeding or nonbreeding season. Home ranges overlapped considerably between species, but overlap in use of individual stands was limited. Relative area of 4 canopy-cover classes (<20, 20–39, 40–59, and≥60% canopy cover) and 3 cover types (ponderosa pine forest, pine-oak forest, and meadow) did not differ between ranges of spotted and great horned owls in either season. Use of canopy-cover classes differed between species in both seasons, however, and use of cover types differed during the breeding season. In general, great horned owls used meadows and open stands (canopy cover <40%) more than spotted owls, who roosted and foraged primarily in forests with ≥40% canopy cover. Structural characteristics of forest stands within the home range also differed between species, as did characteristics of stands used for foraging and roosting. Differences in structural characteristics were consistent with observed differences in use of canopy-cover classes and cover types; stands used by great horned owls had lower log volume, less shrub and canopy cover, and greater herbaceous cover than stands used by spotted owls. The observed patterns of habitat use are consistent with morphological features suggesting that great horned owls are adapted to hunt in more open habitats than spotted owls. Our results suggest that silvicultural treatments that reduce canopy cover below 40% or create large openings within the forest will likely favor great horned owls, whereas maintenance of closed-canopy stands (canopy cover ≥60%) should favor spotted owls. Such stands were rare in our study area, arguing for their conservation where they occur.

Key words: Arizona, *Bubo virginianus*, great horned owl, habitat use, home range, Mexican spotted owl, pine-oak forest, radiotelemetry, *Strix occidentalis lucida*

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INTRODUCTION

The Mexican spotted owl (*Strix occidentalis lucida*) inhabits forested mountains and canyon terrain throughout much of the southwestern United States and northern Mexico (Ward et al. 1995). It is often associated with older forests or forests with relatively complex structure (Ganey and Balda 1994, Ganey and Dick 1995, Seamans and Gutiérrez 1995) and was listed as threatened in 1993 because of concerns over the effects of timber harvest on the amount and distribution of such forests in the southwest (Fed. Register 58: 14248–14271). Specific concerns leading to designating this owl as threatened included: (1) loss of habitat where timber harvest simplified forest structure; and (2) fragmentation of remaining spotted owl habitat due to habitat loss. Fragmentation could increase predation rates on spotted owls by favoring predators suspected to favor edges or more open landscapes, such as the great horned owl (*Bubo virginianus*) (Forsman and Bull 1989, Fed Register 58: 14268). Little information is available, however, on comparative habitat use by Mexican spotted and great horned owls, interactions between these owls, or the effects of timber harvest on populations of either owl.

The Mexican spotted owl is most common in mixed-conifer forests, rocky canyonlands, or pine-oak forests (Ganey and Dick 1995). Home-range size of Mexican spotted owls varies among habitat types and geographic areas (Ganey and Dick 1995), but data are lacking for many habitat types and areas. Data on habitat selection within home ranges of Mexican spotted owls are limited to a single study (Ganey and Balda 1994).

The great horned owl is widespread in western North America and occupies habitats ranging from boreal forests to deserts (Forsman and Bull 1989). No information is available on home-range size or habitat-use patterns of great horned owls in the southwestern United States. Forsman and Bull (1989) speculated that some types of timber management might increase numbers of great horned owls, potentially leading to increased predation on spotted and other owls. Landscapes associated with great horned owls in Oregon contained more shrub/forb habitat, more stands harvested under shelterwood logging systems, less mature/old-growth forest, less interior forest habitat, and a higher ratio of edge to mature/old growth forest than landscapes associated with northern spotted owls (*S.o. caurina*; Johnson 1993).

No quantitative data exist to document the above relationships within the range of the Mexican spotted owl. Anecdotal

Fig. 1. Map showing the location of Arizona within the USA, and the location of the study area (black rectangle) within Arizona.

evidence suggests that spotted owls may avoid or abandon areas occupied by great horned owls (Phillips et al. 1964, Kertell 1977, Johnson and Johnson 1985). In contrast, Ganey (1988) reported hearing great horned owls calling within all five home ranges of radiotagged spotted owls studied in northern Arizona.

The great horned owl preys on spotted owls (Forsman et al. 1984, Miller 1989) and may compete with spotted owls for resources such as food and nest sites. Effects of competitive and predatory interactions between species have been documented in other owls (Hakkarainen and Korpimäki 1996), but little to no data exist to evaluate such interactions between spotted and great horned owls.

To provide information on comparative patterns of habitat use between spotted and great horned owls, we evaluated home-range size and habitat use of these owls in northern Arizona.

Table 1. Home-range size of radiotagged Mexican spotted and great horned owls in ponderosa pine- Gambel oak forest, northern Arizona, 1990–1993. *n* — number of individual owls included in estimates.

Season	Home-range size (ha)					
	Mexican spotted owl			Great horned owl		
	n	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*
Breeding	8	392.5	70.0	3	394.0	150.6
Nonbreeding	14[1]	948.9	146.8	4	889.0	120.2
Annual	12	895.0	119.4	4	721.5	77.5

[1] Fourteen ranges calculated for thirteen individual owls. One female moved to a new territory during the study. Separate ranges were estimated for both territories (in different years).

Specific objectives included: (1) estimate home-range sizes of both species; (2) estimate spatial overlap among home ranges between species; and (3) compare habitat-use patterns between species.

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STUDY AREA

The study area was located within the Bar-M and Woods Canyon watersheds, Coconino National Forest, approximately 40 km south of Flagstaff, Arizona (Fig. 1). Elevation on the study area ranged from 1,850–2,440 m. Topography was relatively gentle with rolling terrain broken by scattered volcanic buttes and small canyons.

Most of the study area consisted of ponderosa pine (*Pinus ponderosa*; plant names follow Brown, 1982) forest with scattered meadows or parks. Gambel oak (*Quercus gambelii*) was a common associate in forested areas. Alligatorbark juniper (*Juniperus deppeana*) was present in many stands, particularly on warmer, drier sites. Small pockets of quaking aspen (*Populus tremoloides*) also occurred throughout the study area, and small numbers of narrowleaf cottonwood (*P. angustifolia*) and boxelder (*Acer negundo*) occurred in some canyons. Major shrub species included New Mexican locust (*Robinia neomexicana*), buckbrush (*Ceanothus fendleri*), and Arizona rose (*Rosa arizonica*).

Most of the study area had experienced some form of logging, although some areas had not been logged within the last 30 yrs. In areas with recent logging, silvicultural methods varied from light selection cutting to heavy seed-tree cuts. Final removal had occurred in few stands, however. Because of silvicultural activities and natural variation, forests on the study area were uneven-aged and ranged from very open to relatively dense. Consequently, it was impossible to group these forests into discrete categories based on tree size or age.

METHODS

Radiotelemetry

We captured owls using noose poles, mist nets (Forsman 1983) and bal-chatri traps (Bloom 1987). Radio transmitters

Table 2. Home-range overlap (%) among neighboring Mexican spotted and great horned owls in pine-oak forest, northern Arizona, 1990–1993. Estimates based on 95% adaptive kernel home ranges.

Category	Season					
	Breeding			Nonbreeding		
	n	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*
% spotted owl range shared with other spotted owls[1]	8	9.3	4.3	14	3.0	4.8
% great horned owl range shared with other great horned owls[1]	3	0.3	0.2	4	16.7	6.1
% Mexican spotted owl range shared with great horned owls	6	51.0	24.3	12	74.1	4.8
% great horned owl range shared with Mexican spotted owls	3	57.4	12.2	4	70.5	12.3

[1] Excluding the mate.

(Communication Specialists Inc., Orange, CA, or Telonics Inc., Mesa, AZ) were attached using a backpack harness constructed of 6-mm tubular teflon ribbon. Transmitter packages weighed approximately 18 g. Radio signals were received using 3-element Yagi antennas and Icom IC-H16 receivers (Communication Specialists) modified for radiotelemetry reception.

Owls were tracked 3–6 days and nights per week throughout the year and were located at all hours of the day and night. We attempted to minimize autocorrelation between subsequent locations (Swihart and Slade 1985) by using only one location per individual per day or night in analyses. All nocturnal locations were assumed to represent foraging activity, and all diurnal locations were classified as roosting locations (Forsman et al. 1984). Locations of females on nests were not used in analyses.

Nocturnal locations were based on triangulation of compass bearings to the radiotagged owl from ≥3 known locations. Fixed tracking points were established at intervals of 0.16–0.32 km along roads. We accepted locations only if ≥3 bearings formed an intersection polygon <2 ha in size. For intersection polygons >2 ha in size we estimated bearings from different tracking points until a suitable polygon was obtained. We assumed that the owl was located at the center of the intersection polygon.

When locating spotted owls during the day, we first estimated the owls position by triangulation then visually observed the owl on its roost. For convenience, we refer to these as double-sampled roost locations. We compared the visual and triangulated locations to estimate accuracy of triangulated locations (Carey et al. 1990). This provides only a rough estimate of accuracy for foraging locations, because animal movement can also affect accuracy of triangulations (Schmutz and White 1990). This procedure was not used on great horned owls because they usually flushed on approach of the observer.

Home-range characteristics

We estimated home-range size using the program TELEM (McKelvey 1993). We use the term home range to refer to an area consistently used by an animal in its day to day activities (Burt 1943). All home-range estimates are artificial constructs, and all have their limitations (Boulanger and White 1990). We used a 95% adaptive kernel (Worton 1989) estimate of home-range size in all analyses. We chose this estimator for three reasons. First, the adaptive kernel estimator requires no unrealistic assumptions about the utilization distribution (Worton 1989). Second, it outperformed other home-range estimators in simulations using data with known spatial properties (Worton 1995, see also Boulanger and White 1990). Third, we wished to use home range areas to estimate relative availability of habitats. The adaptive kernel estimator generally does not include large areas of unused habitat, and therefore should give a more conservative estimate of which habitats are available to the animal than most home-range estimators.

Separate estimates of home-range size were computed for breeding-season (1 March – 31 August), nonbreeding-season (1 September – 28 February), and annual ranges for both individuals and pairs. Locations were pooled among years because area used varied little among years. Because small sample sizes (<50; K. S. McKelvey pers. comm.) or short tracking periods could result in biased estimates of home-range size, we estimated seasonal home ranges for individuals only where the number

Table 3. Use of forest stands by Mexican spotted and great horned owls within zones of interspecific home-range overlap in pine-oak forest, northern Arizona, 1990– 1993.

Season	Activity	No. of stands	% of stands used by			
			Both species	Neither species	Spotted owls only	Great horned owls only
Breeding	Foraging	63	30.2	34.9	30.2	4.8
Breeding	Roosting	63	6.3	54.0	6.3	33.3
Nonbreeding	Foraging	152	25.0	38.8	24.3	11.8
Nonbreeding	Roosting	152	15.1	49.3	16.5	19.1

Table 4. Contrasts run on home-range composition and use of habitat categories by Mexican spotted and great horned owls in pine-oak forest, northern Arizona, 1990–1993. Home-range composition refers to relative area (%) in different categories. All analyses used multiresponse permutation procedure (Slauson et al. 1991). Sample sizes were 8 and 14 spotted owls and 3 and 4 great horned owls for breeding and nonbreeding seasons, respectively.

Contrast	p-value
Home-range composition, between species	
a. Canopy cover, breeding season	0.735
b. Canopy cover, nonbreeding season	0.633
c. Cover type, breeding season	0.237
d. Cover type, nonbreeding season	0.904
Use of canopy classes, between species	
a. Breeding season, foraging	0.062
b. Nonbreeding season, foraging	0.049
c. Breeding season, roosting	<0.001
d. Nonbreeding season, roosting	0.293
Use of cover types, between species	
a. Breeding season, foraging	0.022
b. Nonbreeding season, foraging	0.353
c. Breeding season, roosting	0.029
d. Nonbreeding season, roosting	0.098

of radio locations was ≥80 and the owl was tracked for ≥5 months during that season. We used Spearman's rank correlation coefficient (r_s; Conover 1980) to examine the relationship between number of locations and home-range estimates. We compared seasonal home-ranges between species using Mann-Whitney tests (Conover 1980).

Overlap in home range among all adjacent individuals of both species was calculated for seasonal and annual ranges (% overlap = [area shared/total home-range area] × 100). We compared nearest-neighbor distances between nests of conspecifics with those of heterospecifics using Welch's test to account for unequal sample sizes and heterogeneous variances (Milliken and Johnson 1984).

Habitat-use patterns

We assessed habitat-use patterns at scales ≥individual forest stands using stands delineated by the U.S. Forest Service (USFS). These stands are intended to represent homogeneous units of vegetation. We focused on this scale because: (1) land management is often conducted at this scale; (2) no previous studies of habitat characteristics of Mexican spotted owls have focused at this scale (Ganey and Dick 1995); (3) little information is available on characteristics of foraging areas used by spotted owls (Ganey and Dick 1995); and (4) assessing habitat characteristics of foraging areas at finer scales was impossible due to potential inaccuracies in triangulated locations.

Use of forest stands. We quantified use of stands by individual owls by overlaying owl locations on USFS stands using a geographical information system (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, CA). Stand use was standardized as locations/ha by dividing the number of locations within a stand by the area of that stand contained within the 95% adaptive kernel contour. We excluded stands with <4ha of their area contained within the home range from analyses, because telemetry accuracy precluded an accurate assessment of use of such stands. These stands were typically intersected by the boundary of the home range and showed little or no evidence of use by owls.

We assessed error rates in assigning owl locations to stands by overlaying double-sampled roost locations on the stand coverage and computing the percentage of locations where triangulated and visual locations fell within different stands. We tested for differences in error rates among spotted owl pairs using a chi-square goodness-of-fit test (Conover 1980). We used pair as the sampling unit because accuracy of locations could be influenced by local topography and vegetation (Samuel and Fuller 1994).

For stands where home ranges of great horned and spotted owls overlapped, we estimated proportions used by both species, only one species, or neither species. These stands could be used by either species, and this estimate of overlap in stands used might thus be more informative than spatial overlap in home-range area.

Sampling of stand characteristics. We used the boundaries of spotted owl home ranges to define a sampling frame for estimating habitat characteristics within stands. Habitat characteristics were sampled on a series of plots located at 200-m intervals on a grid laid out along a randomly-selected bearing from a known starting point (a road junction). Sampling effort was based on the estimated number of samples required to accurately estimate snag density (see Bull et al. 1990), the characteristic expected to show the greatest variability.

Habitat characteristics were sampled using both variable- and fixed-radius plot sampling. Plot centers were located along the random bearing. From plot center, basal area of trees and snags was estimated using basal area factor (BAF) prisms (Avery and Burkhart 1983; BAF 20 for trees; BAF 5 for snags). All trees and snags sampled by the BAF prisms were identified to species, and diameter at breast height (dbh) was measured (nearest cm) using a diameter tape.

Variables representing ground and foliage cover were sampled along a 36-m line transect centered at plot center and oriented in a random direction. Point intercepts were sampled at 1-m intervals along the transect. At each intercept, we recorded the type of ground cover (vegetation, litter, dead wood, or rock), and the presence/absence of above-ground foliage in three height categories (≤1 m, 1–2 m, and >2 m). We refer to these as low-shrub, medium-shrub, and canopy cover, respectively. All cover variables were converted to percentages for analysis.

We recorded midpoint diameter (cm) and total length (0.1 m) of all log segments ≥15 cm midpoint diameter and ≥2 m in length contained within boundaries of 0.1-ha plots. Log volume (m^3/ha) was calculated assuming cylindrical shape.

Habitat variables were averaged across plots within stands to estimate mean stand characteristics and their variability.

Table 5. Relative area and use (%) of canopy-cover classes within the home ranges of radiotagged Mexican spotted and great horned owls. Shown are means and standard errors (in parentheses). n = 8 and 14 spotted owls and 3 and 4 great horned owls during the breeding and nonbreeding seasons, respectively.

Canopy class (%)	Species					
	Mexican spotted owl			Great horned owl		
	Available	Foraging use	Roosting use	Available	Foraging use	Roosting use
Breeding season						
<20	7.4 (2.2)	13.9 (1.9)	1.7 (0.8)	14.7 (7.9)	22.3 (14.8)	18.7 (12.9)
20–39	34.1 (6.5)	23.5 (4.9)	7.5 (2.8)*	44.1 (18.8)	56.1 (18.4)	45.7 (18.6)*
40–59	38.6 (3.0)	25.6 (4.8)	5.8 (2.8)	31.1 (8.5)	19.0 (10.5)	27.5 (20.2)
≥60	19.9 (4.5)	36.7 (6.7)	85.0 (4.8)*	10.1 (2.9)	2.6 (1.6)	8.1 (3.0)*
Nonbreeding season						
<20	13.4 (2.8)	14.3 (2.3)	11.2 (2.2)	9.3 (7.3)	8.1 (1.7)	9.6 (4.9)
20–39	43.0 (5.2)	31.4 (4.5)	24.7 (3.9)	57.2 (14.7)	62.9 (10.8)	52.3 (13.7)
40–59	35.3 (2.6)	37.0 (2.3)	33.6 (3.8)	28.8 (7.3)	27.3 (8.2)	32.4 (9.4)
>60	8.4 (1.5)	17.3 (3.8)	30.5 (7.0)	4.6 (1.4)	1.7 (0.9)	5.7 (2.9)

* Indicates use differed significantly ($p<0.013$) between species.

These data then were used both to reclassify stands into discrete categories for further analyses and in direct comparisons of stand characteristics.

Analyses based on habitat categories. We used the data on stand characteristics to create a new GIS coverage based on 4 canopy-cover classes (<20, 20–39, 40–59, and ≥60% canopy cover). We also reclassified stands into 3 cover types. Meadows were defined as open grassy areas ≥4 ha in size. Stands classified as meadow sometimes contained a few scattered trees or included a fringe of trees around the perimeter as delineated by the USFS. Stands where Gambel oak ≥13 cm in diameter at root collar contributed ≥10% of stand basal area or 2.3 m^2/ha were classified as pine-oak forest (Dick et al. 1995). All other stands were classified as ponderosa pine forest. Reclassification of stands resulted in fewer and larger habitat polygons than were present in the original coverage. Therefore, for each coverage we reassessed agreement in polygon assignment between double-sampled roost locations (see above).

We calculated relative area (%) of each category within each home range to quantify composition of home ranges. We compared home-range composition between owl species for each season using multiresponse permutation procedure (MRPP, Slauson et al. 1991). MRPP provides exact estimates of Type I error based on permutations of the actual data rather than assumed population distributions, and has greater power than traditional parametric tests to detect differences in central tendency or dispersion among skewed distributions (Slauson et al. 1991). If home-range composition did not differ significantly between species, we assumed that availability of habitat categories was roughly equal for both species and compared use of habitat categories between species using MRPP. Where overall differences were significant, we used MRPP to determine which categories differed significantly. Probability for significance was set at ($0.05/k$), where k was the number of categories tested (Miller 1966).

Analyses of stand characteristics. Exploratory analyses of stand characteristics were conducted using the variables sampled in habitat plots. We reduced the number of variables by removing one of each pair of highly correlated variables (arbitrarily defined as r_s ≥0.5). This resulted in 10 variables remaining for analysis: snag basal area, coefficient of variation for tree diameters, log volume, live tree basal area, basal area of Gambel oak, percent forb cover, percent rock cover, low-shrub cover, medium-shrub cover, and canopy cover.

We compared characteristics of: (1) all stands within owl home ranges (an assay of range composition); and (2) stands with documented use for roosting or foraging (an assay of habitat use) between species using MRPP. Separate tests were conducted for each season (range composition), or for each combination of season and activity (habitat use).

We used only male spotted owls in the above comparisons because: (1) using both members of pairs would have double-sampled stands within home ranges; and (2) males were less tied to the nest during the breeding season than were females. To standardize comparisons, we used only 4 males for which we had home-range estimates for both seasons. Stands were still included in comparisons twice if they were used by both species of owls or >1 male spotted owl.

We also compared characteristics of nest stands between species, randomly selecting 1 stand/pair where pairs used >1 stand during the study. Following findings of significant overall differences in any analyses involving stand characteristics, we conducted univariate analyses using MRPP and a p-value of <0.005 (0.05/10) for significance.

RESULTS

Thirteen spotted owls and 5 great horned owls were captured and radiotagged during the study. Owls were captured at various times and radiotracked for varying lengths of time depending on owl mortality or equipment malfunction. Three spotted owls were recaptured and equipped with a new radio in subsequent years. Four spotted and no great horned owls died during the study (July 1990 – June 1993). One female was found dead of apparent starvation in January. One male was found laying on the forest floor in May; necropsy failed to identify a cause of death for this owl. We found the intact transmitter harness from another male under a log, but no other remains. The fourth mortality, also a male, appeared to be a case of avian predation, but we were not able to identify the predator.

Home range characteristics

We estimated home-range size during the breeding season for 8 spotted and 3 great horned owls (Table 1). Number of locations for owls included in these estimates averaged 113.0±7.2 (all estimates of variability presented are standard errors) and was not significantly correlated with home range size ($r_s = 0.36$, $p = 0.280$, $n = 11$). Home-range size during the breeding season did not differ significantly between species (Mann-Whitney test, $p = 1.000$).

We estimated home-range size during the nonbreeding season for all individual owls except 1 great horned owl. One female spotted owl moved to a new territory during the study, following the death of her original mate. For this owl, we estimated separate nonbreeding-season ranges for both territories (in different years). Mean sample size for nonbreeding-season estimates was 122.4±7.2 locations/owl and number of locations was not significantly correlated with home-range size ($r_s = 0.15$, $p = 0.550$, $n = 18$). Nonbreeding-season ranges did not differ significantly between species (Mann-Whitney test, $p = 0.959$).

Annual home-range size was estimated for 12 spotted and 4 great horned owls. Mean sample size for individuals included in estimates of annual home-range size was 207.4±17.8 locations/owl; number of locations was not significantly correlated with home-range size ($r_s = -0.05$, $p = 0.860$, $n = 17$). Annual home-range size did not differ significantly between species (Mann-Whitney test, $p = 0.624$).

Home ranges of Mexican spotted owls overlapped with home ranges of conspecifics other than their mates and with home ranges of great horned owls (Table 2). Intraspecific overlap was considerably lower than interspecific overlap. Both intra- and interspecific overlap was lower during the breeding season than during the nonbreeding season. Because not all owls on the study area were radiotagged, all estimates of overlap are biased low.

Most intraspecific overlap occurred along the periphery of the home range, but this was not always the case with interspecific overlap. The nearest-neighbor distance between active spotted and great horned owl nests ($\bar{x} = 930.0\pm124.9$ m, $n = 4$) was significantly less (Welch's test, $p = 0.003$) than the distance between either pairs of spotted owl nests ($\bar{x} = 2832.4\pm274.4$ m, $n = 7$) or pairs of great horned owl nests ($\bar{x} = 3839.3\pm879.1$, $n = 4$). In one instance active great horned and spotted owl nests were separated by only 186 m.

Habitat-use patterns

We sampled habitat characteristics within 2,460 plots representing 328 stands ($\bar{x} = 7.5\pm0.37$ plots/stand). Sampling intensity was approximately 1 plot per 3.4± 0.1 ha. The proportion of double-sampled roost locations in which both the triangulated and visual locations fell within the same stand did not vary significantly among spotted owl pairs ($\chi^2 = 9.4$, $df = 6$, $p > 0.10$). Pooled across spotted owls, polygon assignment was identical for 70.7, 78.9, and 88.4% of 420 double-sampled locations with respect to stand, canopy-cover, and cover-type polygon coverages, respectively.

Table 6. Relative area and use (%) of three cover types within the home ranges of radiotagged Mexican spotted and great horned owls. Shown are means and standard errors (in parentheses). $n = 8$ and 14 spotted owls and 3 and 4 great horned owls during the breeding and nonbreeding seasons, respectively.

Cover type	Species					
	Mexican spotted owl			Great horned owl		
	Available	Foraging use	Roosting use	Available	Foraging use	Roosting use
Breeding season						
Meadow	2.4 (1.1)	1.0 (0.6)*	0.0 (0.0)*	7.9 (2.2)	19.1 (7.1)*	6.8 (2.2)*
Ponderosa pine	36.7 (4.3)	37.8 (8.1)	28.2 (12.9)	45.1 (7.7)	35.0 (7.5)	37.0 (15.2)
Pine oak	60.9 (4.8)	61.2 (8.0)	71.8 (12.9)	47.0 (8.1)	45.9 (0.6)	56.2 (16.2)
Nonbreeding season						
Meadow	2.6 (0.8)	2.1 (0.6)	0.2 (0.2)	3.2 (1.6)	7.1 (3.7)	4.7 (3.0)
Ponderosa pine	37.3 (4.2)	36.7 (6.2)	35.6 (7.5)	47.1 (10.4)	39.3 (9.2)	41.2 (5.8)
Pine oak	60.1 (4.2)	61.2 (6.1)	64.2 (7.6)	49.7 (11.2)	53.6 (9.4)	54.1 (4.4)

* Indicates use differed significantly ($p<0.016$) between species.

Table 7. Contrasts run on characteristics of forest stands within home ranges of Mexican spotted and great horned owls in pine-oak forest, northern Arizona, 1990–1993. All analyses used multiresponse permutation procedure (Slauson et al. 1991). Only male spotted owls (n = 4) were included to avoid double-sampling stands used by both members of owl pairs. Sample sizes for great horned owls were 3 and 4 for breeding and nonbreeding seasons, respectively.

Contrast[1]	p-value
1. All stands within home range, between species	0.001
a. Breeding season	0.014
b. Nonbreeding season	
2. Stands with documented use, between species	
a. Breeding season, foraging	<0.001
b. Breeding season, roosting	<0.001
c. Nonbreeding season, foraging	<0.001
d. Nonbreeding season, rosting	0.035
e. Nest stands	0.031

[1] Numbers of stands included in comparisons, spotted owl followed by great horned owl: 1a = 106, 80; 1b = 272, 142; 2a = 73, 38; 2b = 20, 35; 2c = 136, 64; 2d = 89, 54; 2e = 6, 4.

Overlap in stand use. Most stands contained within zones of interspecific home-range overlap were either not used by either species or were used by only one species (Table 3). Intensity of use (locations/ha) was not significantly correlated between species within stands used by both species (foraging, breeding season: $r_s = -0.088$, $p = 0.721$; foraging, nonbreeding season: $r_s = -0.048$, $p = 0.641$; roosting, breeding season: $r_s = -0.154$, $p = 0.556$; roosting, nonbreeding season: $r_s = 0.026$, $p = 0.830$).

Analyses of habitat categories. Relative area of canopy-cover classes and cover types (i.e. home-range composition) within home ranges of radio-tagged owls did not differ significantly between species for either season (Table 4). In contrast, use of canopy-cover classes differed significantly between species for roosting during the breeding season and foraging during the nonbreeding season. Relative to great horned owls, spotted owls used stands with 20–39% canopy cover significantly less ($p = 0.012$) and stands with ≥60% canopy cover significantly more ($p<0.001$) for roosting during the breeding season (Table 5). Use of individual categories did not differ between species for foraging during the nonbreeding season. Use of canopy-cover classes for roosting did not differ significantly between species during the nonbreeding season (Table 4). Use of canopy classes for foraging was almost significantly different between species during the breeding season (Table 4). Given the small sample of great horned owls and limited permutations of the data possible, this may indicate that differences exist in use of foraging habitat during the breeding season. If so, however, we lacked the statistical power required to detect those differences.

Use of cover types differed between species for both foraging and roosting during the breeding season (Table 4). Great horned owls used meadows significantly more than spotted owls for both activities (Table 6; $p = 0.002$ for foraging and 0.001 for roosting). Use of cover types did not differ significantly between species during the nonbreeding season.

Analyses of stand characteristics. Characteristics of stands contained within home ranges of great horned and male spotted owls differed significantly in both seasons (Table 7). Log volume ($p = 0.004$) and coefficient of variation of tree diameters ($p = 0.003$) were significantly greater on stands in home ranges of spotted owls during the breeding season. No individual variables differed between species during the nonbreeding season.

Characteristics of stands used for foraging also differed between species in both seasons (Table 7). Log volume and low-shrub cover were significantly greater (p-values <0.001) in foraging stands used by spotted owls than in those used by great horned owls during the breeding season. During the nonbreeding season, log volume ($p<0.001$), low- and medium-shrub cover (both p-values = 0.001), and canopy cover ($p<0.001$) were significantly greater on foraging stands used by spotted owls, whereas stands used by great horned owls had greater percent forb cover ($p = 0.002$). Characteristics of stands used for roosting and nesting also differed between species in both seasons (Table 7), but no individual variables differed significantly in either season.

DISCUSSION

Home ranges of Mexican spotted and great horned owls overlapped broadly on our study area, but overlap in habitat use was low between species. Great horned owls used meadows more and forested stands less than spotted owls. They concentrated use in stands with <40% canopy cover, whereas spotted owls primarily used stands with ≥40% canopy cover (Table 5).

Reasons for this habitat partitioning are unknown. It could indicate avoidance behavior on the part of one or both species, but we have no evidence to support this hypothesis. It could also simply be a result of both species foraging in the habitats to which they are best adapted. For example, great horned owls have relatively large eyes, a well-developed temporal fovea (Johnsgard 1988), and lack the asymmetrical ears and associated facial disc associated with accurate location of prey by sound (Konishi 1983). They were more crepuscular than other sympatric owls in Colorado, were able to locate prey visually at low light levels (Marti 1974), and have the highest wing loading reported for North American owls (Johnsgard 1988, Table 5). These morphological and behavioral features suggest that great horned owls may be most effective hunting visually in relatively open habitats.

In contrast, the spotted owl has asymmetrical ears, a well-developed facial disc, and low wing loading. These features are typical of forest owls that can hunt effectively by sound (Norberg 1987), and Miller (1974) observed spotted owls capture prey from areas that were not visible from their perch. The ability to locate prey by sound would facilitate foraging in the denser forests used by spotted owls in this study. Thus, the observed habitat partitioning may be driven more by innate foraging behavior than by avoidance behavior, at least in a proximate sense. The ultimate factors driving the evolution of morphological and behavioral adaptations for foraging are beyond the scope of this study.

Regardless of the mechanisms driving the observed patterns of habitat use, these patterns have important implications for forest managers. Our results do not support the hypothesis that past management has increased habitat suitability for either species of owl in this area. Historical evidence suggests that closed-canopy forests were rare in this area, and that the combined effects of logging, fire suppression, and livestock grazing resulted in increases in forest density and canopy cover, encroachment of trees on meadows, and a change in forest age structure from dominance by large old trees to dominance by small young trees (Covington and Moore 1994, USDI 1995). Thus, the habitats (meadows and open stands containing large trees) used most heavily by great horned owls in this study have apparently declined in both area and distribution.

Unlike great horned owls, spotted owls use closed-canopy forests heavily (Table 5), and this has led to claims that amounts of spotted owl habitat have increased as a result of fire suppression (e.g., USDI 1995). A recent analysis of habitat trends failed to support this conclusion, however, and instead noted that the loss of large trees may have been detrimental to spotted owls (USDI 1995). The loss of large oak trees that provide nest cavities for spotted owls may be particularly detrimental (Ganey et al. 1992). The oak component is declining on the study area as large oak trees are lost to senescence, fuelwood harvest, and overtopping by pine forests. At the same time, heavy grazing pressure is maintaining most oak regeneration in juvenile growth stages (USDI 1995).

Finally, both species of owl prey primarily on small mammals that consume herbaceous vegetation and its seeds (Ward and Block 1995, Block and Ganey unpublished data). Production of herbaceous vegetation has decreased as forest density increased (Covington and Moore 1994), suggesting that prey populations and prey diversity may be reduced from historical levels (Reynolds et al. 1996).

Our results do support the hypothesis that future forest management could affect habitat relationships between these species. Treatments that reduce canopy cover below 40% or create openings in the forest are likely to benefit great horned owls, whereas maintenance of closed-canopy stands is more likely to benefit spotted owls.

How much closed-canopy forest spotted owls require in this area is unknown. Closed-canopy stands are relatively rare on the study area (Table 5), suggesting that such stands should be retained where they exist. Historical evidence suggests that such stands were always rare in this area, however (Covington and Moore 1994). Thus, spotted owls may have evolved in a landscape containing relatively few patches of such habitat embedded in a matrix of more open forest. Attempting to manage for closed-canopy stands across much of the landscape may produce forest conditions that cannot be sustained in the long term (Covington and Moore 1994, USDI 1995). As long as such stands are provided on the landscape, management for more open conditions elsewhere may not be detrimental to spotted owls, and may even increase prey populations for both species. This hypothesis should be tested, however, by monitoring trends in landscape composition, prey populations, and spotted owl populations in areas where forest management results in more open stand structures. It may also be desirable to minimize creation of open stands in areas immediately adjacent to spotted owl roosting and nesting stands. Such stands might be used for foraging by both species of owls, particularly if prey populations increase in response to increases in herbaceous vegetation. This could increase opportunities for great horned owls to prey on spotted owls, creating the equivalent of an ecological trap for spotted owls.

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