
Mexican Spotted Owl Home Range and Habitat Use in Pine–Oak Forest: Implications for Forest Management

Joseph L. Ganey, William M. Block, Jeffrey S. Jenness, and Randolph A. Wilson

ABSTRACT. To better understand the habitat relationships of the Mexican spotted owl (*Strix occidentalis lucida*), and how such relationships might influence forest management, we studied home-range and habitat use of radio-marked owls in ponderosa pine (*Pinus ponderosa*)–Gambel oak (*Quercus gambelii*) forest. Annual home-range size (95% adaptive-kernel estimate) averaged 895 ha \pm 70 (SE) for 12 individuals and 997 ha \pm 186 (SE) for 7 pairs of owls. On average, the 75% adaptive-kernel contour (a probability contour containing 75% of the owl locations) included 32 and 30% of the annual home range for individuals and pairs, respectively, suggesting high concentration of activity in a relatively small portion of the home range. Relative area of three covertypes (ponderosapine forest, pine-oak forest, and meadow) did not differ between seasonal ranges, and owls used these covertypes in proportion to their relative area during both breeding and nonbreeding seasons. In contrast, relative area of four canopycover classes varied between seasons. Breeding-season ranges contained greater proportions of areas with canopy cover \geq 60% and lower proportions of areas with 20–39% canopy cover than nonbreeding-season ranges. Owls roosted and foraged in stands with 160% canopy cover more than expected during both breeding and nonbreeding seasons, and used stands with 20–39% canopy cover less than expected except for foraging during the breeding season. Stands used for foraging did not differ in structure between seasons and had greater canopy cover and less rock cover than stands with no documented use. Stands used for roosting differed between seasons in a multivariate comparison, but no individual habitat variables differed between seasons in subsequent univariate comparisons. In both seasons, stands used for roosting had greater canopy cover than stands with no roosting use. Closedcanopy forests, which were used heavily by owls, were relatively rare on the study area, suggesting that such forests warrant special protection in areas managed for spotted owls. This may conflict with efforts to restore more open conditions in ponderosa pine forests. *FOR. SCI.* 45(1):127–135.

Additional Key Words: Gambel oak, habitat use, home range, Mexican spotted owl, pine-oak forest, ponderosa pine, radio telemetry.

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The MEXICAN SPOTTED OWL (*Strix occidentalis lucida*) is widely but patchily distributed throughout forested mountains and canyon terrain in the southwestern United States and northern Mexico (Ward et al. 1995). This subspecies, which is often associated with older forests or forests with relatively complex structure (Ganey and Dick 1995), was listed as threatened in 1993 because of concerns over the effects of timber harvest on the amount and distribution of such forests (Cully and Austin 1993).

The Mexican spotted owl is most common in mixed-conifer forests, but also occurs in rocky canyonlands, encinal oak woodlands, or pine-oak (*Pinus-Quercus*) forests (Ganey and Dick 1995). In this study, we examined home-range size and habitat use of Mexican spotted owls in ponderosa pine (*P. ponderosa* Dougl. ex Laws)-Gambel oak (*Q. gambelii* Nutt.) forest. Although several authors have noted associations between Mexican spotted owls and the presence of oaks (Ganey et al. 1992, Seamans and Gutiérrez 1995, Hodgson 1996), little information exists documenting habitat-use patterns in pine-oak forests. Similarly, home-range size of Mexican spotted owls varies widely among habitat types or geographic areas, but information is lacking for many areas and habitat types, including pine-oak forests (Ganey and Dick 1995). Patterns of habitat use in this forest type are also of interest in a management context. Mexican spotted owls are often associated with closed-canopy forests in other forest types (Ganey and Dick 1995, Grubb et al. 1997). Maintenance of such stands in ponderosa pine forest types may conflict with other management objectives, including restoration of more open stand structures, which were typical in these forest types prior to the era of fire suppression (Covington and Moore 1994).

Study Area

The study area, located 40 km south of Flagstaff, Arizona, was dominated by rolling terrain broken by scattered volcanic buttes and small canyons. Elevation ranged from 1850–2440 m. This study area was of special interest with respect to Mexican spotted owls because it contained no mixed-conifer forest, the most common forest type in which this owl is found throughout its range (Ganey and Dick 1995). Thus, this study area provided an opportunity to study owls in an area where forest composition was greatly different from areas more typically associated with spotted owls.

Ponderosa pine forest was the dominant vegetation type on the study area. Gambel oak was common in many areas, and alligator juniper (*Juniperus deppeana* Steud.) was frequently present on warmer, drier sites. Small pockets of quaking aspen (*Populus tremuloides* Michx.) occurred throughout the study area, with small numbers of narrowleaf cottonwood (*P. angustifolia* James) and box-elder (*Acer negundo* L.) in some drainages. Major shrub species included New Mexican locust (*Robinia neomexicana* Gray), buckbrush (*Ceanothus fendleri*), and Arizona rose (*Rosa arizonica*).

The entire study area was grazed by large numbers of domestic livestock and wild ungulates, and fires had been actively suppressed in this area for approximately a century. Timber harvest had occurred over most of the study area, but

much of the area had no recent (i.e., last 30 yr) history of harvest. In areas with recent logging, silvicultural methods varied from light selection cutting to heavy seed-tree cuts, but final removal had not yet occurred in most stands. Because of forest management, coupled with natural variation, forest stands on the study area were uneven-aged and highly variable in structure. Consequently, it was impossible to classify these stands into discrete structural categories based on tree size or age.

Methods

Field Sampling

Radiotelemetry Methods

We captured owls using noose poles, mist nets (Forsman 1983), or bal-chatri traps (Bloom 1987). Radio transmitters (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 Icom IC-H16 receivers (Communication Specialists) modified for radiotelemetry reception, and handheld 3-element Yagi antennas.

Owls were monitored 3–6 days and nights per week throughout the year and were located at all hours of the day and night. We attempted to reduce spatial 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. Locations of incubating or brooding females were not used in analyses, because nesting females are restricted to the nest area for approximately 2 months.

Nocturnal locations were based on triangulation of compass bearings to the radio-marked owl from ≥ 3 known locations. Fixed tracking points were established at 0.16–0.32 km intervals 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 owls during the day, we first estimated the location by triangulation, and then visually observed the owl on its roost. We refer to these as double-sampled roost locations. We compared the visual and triangulated locations to estimate accuracy of assignment of locations to habitat polygons (see below). This provides only a rough estimate of accuracy for foraging locations, because animal movements at night can also affect accuracy of triangulations (Schmutz and White 1990). Spotted owls generally do not move much during the day.

Habitat Sampling

We characterized habitat within owl home ranges at a fairly coarse scale, because previous experience suggested that triangulated locations were not sufficiently precise to warrant a fine-scale analysis (Ganey and Balda 1994). We used forest "stands" mapped by the USDA Forest Service

(USFS) as our base habitat polygons. These stands were intended to represent homogeneous units of vegetation.

We used the 95% adaptive kernel home range (see Home-Range Size) as the sampling frame for estimating habitats available to owls. Habitat characteristics were sampled on 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, the characteristic expected to show the greatest variability (Bull et al. 1990). All stands ($n = 328$) within owl home ranges were sampled [2,460 plots; $\bar{x} = 7.5 \pm 0.37$ (SE) plots/stand, or 1 plot per 3.4 ± 0.1 (SE) ha].

Habitat characteristics were sampled using both variable- and fixed-radius plots. From plot center, basal area of trees and snags was estimated using basal area factor (BAF) prisms (Avery and Burkhart 1983, p. 185; 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 overhead canopy cover (using a sighting tube). All cover variables were converted to percentages for analysis. All plots were sampled during the summer when deciduous trees had leaves.

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 aggregated across plots within stands to obtain estimates of mean stand characteristics and their variability. These data then were used both to reclassify USFS-typed stands into discrete categories for further analyses and in analyses of owl use versus stand structure (see below).

Data Analysis

General Framework

We had a limited sample of owls, and many of the data sets used were decidedly nonnormal. Because standard transformations did not solve this problem, we used distribution-free tests in most hypothesis tests. For univariate tests, we used exact methods available in SPSS, version 6.1 (Mehta and Patel 1995), with a few exceptions (noted where the relevant analyses are described). For multivariate tests, we used a multiresponse randomized block procedure (MRBP) in program BLOSSOM (Slauson et al. 1991). This procedure is comparable to a randomized-block analysis of variance, but provides estimates of Type I error based on permutations of the data from randomization theory (Edgington 1987) rather than by comparison to an assumed population distribution. Where significant differences were observed in multivariate tests, we conducted sequential univariate comparisons, using MRBP, to determine which categories differed significantly.

Because this amounts to multiple comparisons, we controlled the overall Type I error rate by setting the probability for significance at ($P < 0.05/k$), where k was the number of categories tested (Miller 1966). We blocked by owl in all MRBP analyses, to control for potential differences in availability of habitat characteristics among home ranges and to ensure that all owls were weighted equally in the analysis. Where hypothesis tests included both seasons, only owls for which we estimated home ranges in both seasons (see below) were included. Where hypothesis tests were stratified by season, we included all owls for which we estimated a home range during the relevant season. All estimates of variability presented throughout the paper are standard errors.

Home-Range Size

We estimated home-range size using program TELEM (K.S. McKelvey, 1993, Program Telem. USDA Forest Service, Pacific Southwest Research Station, Albany, Calif.). We use the term home range to refer to an area 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. Briefly, the adaptive kernel (AK) estimator estimates the utilization distribution of a given animal, converts this estimate into a probability density function, then estimates the smallest area containing specified proportions of that probability function (Worton 1995). We chose this estimator for three reasons. First, it requires no unrealistic assumptions about the utilization distribution (Worton 1989). Second, it outperformed most 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 AK estimator generally excludes large areas of unused habitat and therefore provides a more conservative estimate of which habitats are available to the animal than most other estimators. Thus, use of this estimator should make it more difficult to demonstrate habitat selection. This results in a conservative assessment of habitat selection and increased confidence that any selection observed is real and not an artifact of the home-range estimator used.

Separate estimates of home-range (95% AK) and activity-center (75% AK) size were computed for breeding season (March 1–August 31; Ganey and Balda 1989), nonbreeding-season (September 1–February 28), and annual ranges for both individuals and pairs. We used the 75% isopleth to estimate activity-center size because Block et al. (1995:89) reported that this area typically included the nest site as well as the most heavily used roosting and foraging areas. Bingham and Noon (1997) provided additional evidence that a 75% isopleth was appropriate for defining an activity center; over 50% of the northern spotted owls (*S. o. caurina*) they studied had "core areas" adequately resolved between the 60 and 75% adaptive kernel isopleths.

We pooled locations among years for home-range estimates, 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 of radio locations was ≥ 20 and the owl was tracked for at least 5 months during that season. We tested the following hypotheses with respect to home-range size (method in parentheses):

1. Home-range size was not correlated with number of telemetry locations [Spearman's rank correlation coefficient (r_s , Conover 1980); stratified by season].
2. Home-range size did not differ between sexes [Mann-Whitney test (Conover 1980); stratified by season].
3. Home-range size of an individual owl (or pair) did not differ between seasons [Wilcoxon signed-ranks test (Conover 1980)].

Home-Range Composition

We used a geographical information system (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, CA) and a coverage of USFS-delineated forest stands to link the habitat data collected to particular stands. We then used this coverage to create two new GIS coverages. The first reclassified stands into four canopy-cover classes (<20, 20–39, 40–59, and $\geq 60\%$) representing a gradient from very open to relatively closed canopy forest. The second GIS coverage reclassified stands into three cover types (meadow, pine–oak forest, or ponderosa pine forest). We focused on these variables because previous studies indicated that Mexican spotted owls were selective relative to cover types (Ganey and Balda 1994, Seamans and Gutiérrez 1995, Hodgson 1996) or canopy-cover classes (Grubb et al. 1997).

Meadows were defined as open grassy areas ≥ 2.4 ha in size that often contained a few scattered trees. We classified stands as pine–oak forest if Gambel oak ≥ 2.13 cm in diameter at root collar contributed ≥ 2.3 m²/ha or 10% of stand basal area (Dick et al. 1995). All other stands were classified as ponderosa pine forest. We dissolved boundaries between adjacent stands that fell in identical habitat categories, resulting in fewer and larger habitat polygons than were present in the original coverage.

We calculated relative area (%) of each habitat category within each home range to quantify composition of home ranges. We tested the hypothesis that home-range composition did not differ between seasonal ranges, using MRBP with owl as the blocking variable. Briefly, this randomization test considers all owls simultaneously, but compares proportional composition between seasonal ranges of individual owls, rather than averaging composition of seasonal ranges across owls.

Habitat-Use Patterns

We quantified use of habitat polygons by individual owls by overlaying owl locations on the relevant coverage (stands, cover types, or canopy-cover classes). We excluded polygons with <4 ha of their area contained within the home range from analyses, because telemetry accuracy precluded an accurate assessment of use of such polygons. These polygons were "slivers" formed where home-range bound-

aries bisected larger polygons. They were peripheral to owl ranges, and showed little or no evidence of use by owls.

We assessed error rates in assigning owl locations to habitat polygons by overlaying double-sampled roost locations on the relevant coverage and computing the percentage of locations where triangulated and visual locations fell within different polygons. We used a chi-square test (Conover 1980) to test the hypothesis that error rates did not differ among pairs. We used owl pair as the sampling unit because accuracy of locations could be influenced by local topography and vegetation (Samuel and Fuller 1994).

We used MRBP blocked by owl to test the hypothesis that owls used habitat categories (cover types, canopy-cover classes) in proportion to the relative availability of those categories within the home range. Briefly, these randomization tests consider all owls and habitat components simultaneously, but compare proportional use to availability within individual owls rather than summing within these categories across owls. Separate tests were conducted for cover type and canopy cover class, stratified by season (breeding, nonbreeding) and activity (foraging, roosting).

To explore the influence of stand structure on use by owls, we first reduced the number of variables analyzed by removing one of each pair of highly correlated variables (arbitrarily defined as $r_s \geq 0.5$). We retained the variable that we thought might have the most biological relevance to the owl or its prey, based on past studies of Mexican spotted owls and their prey. For example, we retained rock cover because Mexican woodrats (*Neotoma mexicana*), an important prey species (Ward and Block 1995), are associated with presence of rock outcrops. We retained variables pertaining to canopy cover, log volume, and density of trees and snags because previous studies of Mexican spotted owls reported correlations between these types of structural variables and owl use (Ganey and Balda 1994, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Hodgson 1996, Grubb et al. 1997). This resulted in six variables remaining for analysis: canopy cover, live tree density, oak density, snag density, log volume, and percent rock cover. Estimates of tree density included all size classes of trees.

We used MRBP to test the following hypotheses:

1. Stands used by owls did not differ between seasons (stratified by activity).
2. Stands used by owls did not differ from stands with no evidence of owl use.
3. Stands used for foraging did not differ from stands used for roosting (stratified by season).

Where stands used by owls differed significantly between seasons (hypothesis 1), analyses under hypothesis 2 were stratified by season as well; otherwise we pooled seasons for further analyses.

Results

Home Range Size

Thirteen spotted owls were captured and radiotracked for varying lengths of time from 1990–1993. Number of loca-

Table 1. Mean home-range and activity-center size (ha) of radio-marked Mexican spotted owls in northern Arizona. Home-range and activity-center size based on 95 and 75% adaptive kernel (AK) estimates, respectively. Also shown is Spearman's rank correlation coefficient (r_s) between number of locations and the 95% AK estimate, and the percentage of the 95% AK home range included in the activity center, a measure of concentration of activity.

Season	N*	Locations/owl		r_s	P^\dagger	95% AK		75% AK		% of 95% AK ^{††}	
		\bar{x}	SE			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Individual owls											
Breeding	8	122.8	7.8	0.429	0.289	392.5	70.0	121.7	21.8	29.8	3.8
Nonbreeding	14 [‡]	125.6	8.6	0.193	0.528	948.9	146.8	326.5	53.8	33.1	1.6
Annual	12	220.4	20.0	-0.011	0.972	895.0	119.4	301.4	59.1	32.2	1.6
Owl pairs											
Breeding	4	178.5	47.1	0.400	0.600	527.4	86.5	128.9	15.6	28.9	6.2
Nonbreeding	7	243.4	26.7	0.679	0.094	1121.7	170.2	396.6	80.9	33.9	2.6
Annual	7	401.4	70.0	0.571	0.180	996.6	186.2	302.4	66.5	29.7	1.2

• Number of owls or pairs included in estimates.

† P-value from test for relationship between number of locations/owl and 95% AK estimate.

†† Estimated as (75% adaptive kernel size/95% adaptive kernel size)100.

‡ Fourteen ranges calculated for 13 owls. One female switched territories and occupied two distinct home ranges during the study.

tions for owls (or pairs) included in estimates of home-range size was not significantly correlated with home-range size in any season (Table 1), suggesting that range estimates were not artifacts of sampling intensity. Home-range size did not differ significantly between sexes during either the breeding (Mann-Whitney test, $P = 0.486$, $n = 4$ females and 4 males) or nonbreeding seasons ($P = 0.165$, $n = 7$ females and 7 males). Mean annual home-range size was considerably larger for females ($\bar{x} = 1107 \geq 408$ ha, $n = 5$ owls) than for males ($\bar{x} = 673 \geq 294$ ha, $n = 7$ owls). This difference was not quite significant ($P = 0.073$), but the power of this test (and the above tests for differences between sexes within seasons) to detect differences was low due to the small number of owls observed. Nonbreeding-season ranges were significantly larger than breeding-season ranges for both individual owls (Wilcoxon signed-ranks test; $P = 0.008$, $n = 8$ owls) and owl pairs ($P = 0.031$, $n = 4$ pairs; Table 1).

Activity centers (75% adaptive-kernel contours) were relatively small and generally comprised a relatively small part of 95% adaptive-kernel home ranges (Table 1). This pattern was consistent for both individuals and pairs in all seasons.

Home-Range Composition

Relative area of three cover types within the home range did not differ between seasonal ranges (MRBP, $P = 0.619$, $n = 8$ owls). Home ranges were dominated by pine-oak forest in both seasons and contained little area in the meadow cover type (Table 2).

Relative area of four canopy-cover classes differed significantly between seasonal ranges (MRBP, $P = 0.022$,

$n = 8$ owls). Breeding-season ranges contained significantly greater proportions of area with 2–60% canopy cover ($P = 0.006$) and significantly lower proportions of area with 20–39% canopy cover ($P = 0.010$) than did nonbreeding season ranges (Table 3).

Habitat-Use Patterns

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 owl pairs ($\chi^2 = 9.4$, $df = 6$, $P > 0.10$). Of 420 roost triangulations that were checked by double-sampling, 70.7% were correctly classified by stand polygon, 78.9% were correctly classified by canopy-cover polygon, and 88.4% were correctly classified with respect to cover-type polygon.

Use of Cover Types

Use of cover types did not differ from their relative area for either activity type during either season, although results approached significance for roosting use during the nonbreeding season ($P = 0.075$; all other P -values > 0.102). Although we were not able to demonstrate selection for or against particular cover types, the majority of foraging and especially roosting occurred in pine-oak forest, with little use of meadows observed (Table 2).

Use of Canopy-Cover Classes

Considering all canopy-cover classes simultaneously, spotted owls did not use canopy-cover classes in proportion to their relative area within the home range in either season for either activity type (MRBP, all P -values < 0.009). Considering classes individually, owls used the 2–60% canopy

Table 2. Relative area and use (%) of three cover types within the home ranges of radio-marked Mexican spotted owls. $N = 8$ and 14 owls during the breeding and nonbreeding seasons, respectively.

Cover type	Breeding season						Nonbreeding season					
	Percent of home range		Percent of locations				Percent of home range		Percent of locations			
	\bar{x}	SE	Foraging		Roosting		\bar{x}	SE	Foraging		Roosting	
Meadow	2.4	1.1	1.0	0.6	0.0	0.0	2.6	0.8	2.1	0.6	0.2	0.2
Ponderosa pine	36.7	4.3	37.8	8.1	28.2	12.9	37.3	4.2	36.7	6.2	35.6	7.5
Pine-oak	60.9	4.8	61.2	8.0	71.8	12.9	60.1	4.2	61.2	6.1	64.2	7.6

Table 3. Relative area and use (%) of canopy-cover classes within the home ranges of radio-marked Mexican spotted owls. *N* = 8 and 14 spotted owls during the breeding and nonbreeding seasons, respectively.

Cover (%)	Breeding season						Nonbreeding season					
	Percent of home range		Percent of locations				Percent of home range		Percent of locations			
	\bar{x}	SE	Foraging		Roosting		\bar{x}	SE	Foraging		Roosting	
< 20	7.4	2.2	13.9	1.9	1.7	0.8	13.4	2.8	14.3	2.3	11.2	2.2
20–39	34.1	6.5	23.5	4.9	7.5	2.8*	43.0	5.2	31.4	4.5*	24.7	3.9*
40–59	38.6	3.0	25.6	4.8*	5.8	2.8*	35.3	2.6	37.0	2.3	33.6	3.8
≥ 60	19.9	4.5	36.7	6.7*	85.0	4.8*	8.4	1.5	17.3	3.8*	30.5	7.0*

* Indicates that use of the canopy-cover class differed significantly from use expected based on relative area of that class. This comparison was blocked by owl; significance level for comparisons of individual canopy-cover classes was set at $P < 0.0125$ (= **0.0514**).

class more than expected for both foraging and roosting in both seasons (Table 3). Use of this class for roosting during the breeding season was particularly pronounced. Owls used the 40–59% canopy class as expected during the nonbreeding season, but used this class less than expected during the breeding season. Owls used the 20–39% canopy class less than expected for roosting in both seasons and for foraging during the nonbreeding season. Owls used the < 20% canopy class in proportion to its relative area in both seasons for both roosting and foraging.

Stand Characteristics

Characteristics of stands used for foraging did not differ between seasons (MRBP, $P = 0.56$, $n = 8$ owls). Consequently, we pooled foraging stands across seasons for comparisons with stands with no documented use. Considering all six habitat variables simultaneously, stands used for foraging differed significantly from stands with no documented foraging use ($P = 0.002$). Subsequent univariate comparisons indicated that stands used for foraging had greater canopy cover ($P < 0.001$) and lower rock cover ($P = 0.003$) than stands with no documented use (Table 4).

Characteristics of stands used for roosting differed between seasons when all six habitat variables were considered (MRBP, $P = 0.024$, $n = 8$ owls), but no variables differed significantly (at $P < 0.008$) between seasons in univariate comparisons (Table 5). Stands used for roosting differed from stands with no documented use in both seasons ($P = 0.030$ and 0.001 for multivariate comparisons during breed-

ing and nonbreeding seasons, $n = 8$ and 14 owls, respectively). Stands used for roosting had greater canopy cover than stands not used for roosting during both the breeding season and nonbreeding season (Table 5).

Stands used for foraging differed significantly from stands used for roosting during the breeding season (MRBP, $P = 0.01$, $n = 8$ owls), but not during the nonbreeding season ($P = 0.068$, $n = 14$ owls). Stands used for roosting during the breeding season had greater canopy cover ($P = 0.007$) and density of live trees ($P = 0.003$) than stands used for foraging.

Discussion

This study provides the first description of Mexican spotted owl habitat-use patterns in ponderosa pine–Gambel oak forest, and thus provides important information for land managers charged with integrating management of spotted owl habitat with other land-management objectives. Annual home ranges of Mexican spotted owls in this forest type are among the largest reported in this subspecies; only home ranges in the canyonlands of southern Utah are similar in size [$\bar{x} = 882 \pm 612$ (SD) ha for individual owls, using the same AK estimator (Willey 1998)]. As in other studies of Mexican spotted owls (Ganey and Balda 1989, Zwank et al. 1994, Willey 1998), activity was concentrated in a relatively small part of the home range (Table 1), but these activity centers were relatively large because of the large overall size of home ranges. Block et al. (1995:86) recommended protecting a 243 ha area around occupied nest areas of Mexican spotted

Table 4. Selected characteristics of stands within the home range used and not used for foraging by radio-marked Mexican spotted owls in pine–oak forest, northern Arizona. Based on 328 stands, of which 190 were used for foraging.

Variable	Used		Unused		P*
	\bar{x}	SE	\bar{x}	SE	
Log vol (m ³ /ha)	21.0	2.3	19.2	2.5	0.482
Snags/ha	18.8	1.6	19.2	2.1	0.705
Live trees/ha	451.2	27.0	449.9	27.7	0.879
Live tree basal area (m ² /ha) [†]	24.8	0.3	23.3	0.7	0.019
Oaks/ha	71.5	7.9	53.1	6.8	0.050
Oak basal area (m ² /ha) [†]	3.3	0.2	2.5	0.2	0.022
Rock cover (%)	16.5	1.2	18.4	1.3	0.003
Canopy cover (%)	42.9	1.2	38.8	1.3	< 0.001

* P-value resulting from a blocked (by owl) comparison of stands used vs. not used for foraging. Significance level for univariate comparisons set at $P < 0.008$ (= **0.0516**).

[†] Indicates variables not used in multivariate comparison of stands used vs. not used, because both were correlated with canopy cover. These variables are reported here because they are considered biologically meaningful.

Table 5. Selected characteristics of stands within the home range used and not used for roosting by 8 and 14 radio-marked Mexican spotted owls during the breeding and nonbreeding seasons, respectively, in northern Arizona. Numbers of stands used and not used shown in parentheses.

Variable	Breeding season				P*	Nonbreeding season				P*	P _i [†]
	Used (34)		Unused (119)			Used (138)		Unused (190)			
	\bar{x}	SE	\bar{x}	SE		\bar{x}	SE	\bar{x}	SE		
Log volume (m ³ /ha)	22.0	2.5	18.3	3.3	0.476	21.5	2.2	19.2	2.5	0.061	0.381
Snags/ha	21.1	2.8	21.3	4.0	0.775	16.8	1.1	19.5	2.0	0.193	0.144
Live trees/ha	482.2	45.2	454.5	45.8	0.556	453.5	22.8	434.7	22.4	0.537	0.113
Live tree basal area (m ² /ha) ^{††}	28.2	0.3	24.1	0.9	0.008	25.2	0.5	23.4	0.5	0.007	0.004
Oaks/ha	104.6	36.7	65.3	12.3	0.266	72.3	8.8	54.3	6.6	0.072	0.208
Oak basal area (m ² /ha) ^{††}	4.7	0.8	2.6	0.2	0.033	3.5	0.2	2.5	0.1	0.006	0.055
Rock cover (%)	13.5	2.2	16.6	2.3	0.025	17.2	1.4	17.8	1.1	0.333	0.032
Canopy cover (%)	53.2	3.1	39.4	1.2	0.008	44.1	1.1	38.7	1.4	<0.001	0.019

• P-value resulting from a blocked (by owl) comparison of stands used vs. not used for roosting. Significance level for univariate comparisons set at $P < 0.008$ (= 0.05/6).

† P_s = P-value resulting from a blocked (by owl) comparison of stands used for roosting between seasons. Significance level for univariate comparisons set at $P < 0.008$ (= 0.05/6).

†† Indicates variables not used in multivariate comparisons, because both were correlated with canopy cover. These variables are reported here because they are considered biologically meaningful.

owls, based on estimates of activity-center size for owls in various forest types. This approach would protect only 86% of the median (284 ha) and 80% of the mean (302 ha) activity center observed in our study. Therefore, we recommend that managers protect larger areas where owls occur in pine-oak forest.

We believe that our approach to estimating habitat selection was relatively conservative. We used a home-range estimator that fits the distribution of animal locations closely and thus does not include large amounts of unused habitat. This should make it harder to demonstrate selection for habitats, because much of the selection process may already be accounted for in the home-range estimate. We used statistical procedures that required no unrealistic assumptions about the distribution of sample data, and we included only owls for which we had large numbers of locations (≥ 80) in analyses, which increases the power of these analyses (White and Garrott 1986, Samuel and Kenow 1992). We required low P-values for significance in multiple comparisons, making it difficult to demonstrate selection for particular variables or categories. Finally, owl locations were subject to errors in assignment to habitat polygons ranging from approximately 12% for cover types to almost 30% for stands. Locational errors also make it harder to demonstrate habitat selection (White and Garrott 1986, Samuel and Kenow 1992).

Despite these factors, we observed selection by owls for particular canopy-cover classes and stand characteristics. Results were particularly striking for use of canopy-cover classes by roosting owls during the breeding season, with mean use of the $\geq 60\%$ canopy-cover class over four times greater than its relative area (Table 3). This pattern may be partly driven by the fact that owls tend to nest in closed-canopy stands and often roost near the nest during the breeding season. However, although most pairs of owls bred successfully at some point during the study, pairs also were monitored in years when they did not nest. These owls were not tied to a nest location and did not always roost in former

nest stands, yet still roosted in closed-canopy forests.

Canopy cover also emerged as an important variable in analyses comparing characteristics of used vs. unused stands. It was the only variable that varied significantly in all analyses, providing further evidence that owls are highly selective with respect to canopy cover, particularly with respect to roosting areas during the breeding season. These results are consistent with previous studies, including studies in other forest types, indicating that Mexican spotted owls nest and roost primarily in closed-canopy forests and in some cases forage selectively in such forests (Ganey and Balda 1994, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Grubb et al. 1997).

In contrast, although owl home ranges were dominated by pine-oak forest and owls used pine-oak forest extensively, we were not able to demonstrate habitat selection with respect to forest cover types. This could indicate that owls were not selecting for pine-oak forest as defined here. It could also indicate that selection for pine-oak forest had already occurred at the home-range scale, as indicated by the fact that it comprised $\geq 60\%$ of home-range area during both seasons. Our subjective impression was that pine-oak forest comprised far less than 60% of the overall landscape. Unfortunately, no reliable data exist that would allow us to quantify relative amounts of pine-oak forest in the overall landscape, so we cannot test this hypothesis.

Although we were not able to demonstrate selection for pine-oak forest, several lines of evidence suggest that the oak component can be quite important to owls in our study area. First, stands used for foraging and roosting typically had greater density and basal area of Gambel oak than unused stands (Tables 4 and 5). Second, Gambel oak contributed greatly to canopy cover and canopy layering within stands; both appear to be habitat features of importance to the owls. Finally, abundance of several prey species taken by Mexican spotted owls was correlated with density and/or basal area of Gambel oak (Ward and Block 1995). Consequently, we recommend that the oak

component be maintained or enhanced in areas where owls occur. This could be accomplished by eliminating harvest of large oak trees for fuelwood and reducing grazing pressure, by both wildlife and livestock, to allow for greater recruitment of oak (Block et al. 1995, p. 100–101).

In general, our results suggest that areas managed for owl roosting/nesting habitat in pine-oak forest should have canopy cover $\geq 60\%$ (Table 3), high basal area of live trees, and a well-developed oak component. We recommend managing such stands for at least mean values of live tree and oak basal area observed in stands used for roosting during the breeding season (Table 5). Canopy cover within roost stands was more tightly linked to basal area than to tree density ($r_s = 0.62$ vs. 0.47), suggesting that maintaining a large-tree component in these stands is likely more important than simply maintaining dense stands lacking a large-tree component.

Implications for Restoration of Ponderosa Pine Forests

Because past management practices in ponderosa pine forests have altered habitat conditions profoundly, considerable interest has focused on restoring these forests to “presettlement” conditions (Covington and Moore 1994). This would generally result in great reductions in tree density, basal area, and canopy cover (Covington and Moore 1994). Our results suggest that treatments of this nature are not compatible with maintaining roosting habitat for spotted owls.

Does this mean that maintaining spotted owl habitat is incompatible with restoring ponderosa pine forests? Perhaps not. There is evidence that some ponderosa pine forests escape the frequent surface fires that maintain open stands, developing into closed-canopy forests subject to stand-replacing disturbance events such as large wildfires (Arno et al. 1995, Shinneman and Baker 1997). Thus, closed-canopy stands may be within the natural range of variability for ponderosa pine forests. Historical evidence suggests that such stands were rare in this area (Covington and Moore 1994), and our results suggest that they are still relatively rare. Areas occupied by spotted owls generally contain greater amounts of closed-canopy forest than surrounding areas (Grubb et al. 1997), yet stands with canopy cover $\geq 60\%$ comprised only 20 and 8% of breeding- and nonbreeding-season home-range areas, respectively. Thus, Mexican spotted owls may have evolved in a landscape containing relatively few patches of such habitat embedded in a matrix of more open forest. As long as such patches are maintained on the landscape, management for more open stand structures elsewhere may be compatible with efforts to maintain and recover owl populations. We recommend that initial restoration treatments avoid areas occupied by spotted owls, however, because managers have limited experience with restoration treatments and because the effects of such treatments on spotted owls are unknown. This should leave considerable areas available for restoration, because spotted owls do not occur widely in ponderosa pine forests (Ganey and Dick 1995).

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