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ROOST SITES OF RADIO-MARKED MEXICAN SPOTTED OWLS IN ARIZONA AND NEW MEXICO: SOURCES OF VARIABILITY AND DESCRIPTIVE CHARACTERISTICS

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ABSTRACT.—To increase understanding of roosting habitat of Mexican Spotted Owls (*Strix occidentalis lucida*) and factors that influence use of roosting habitat, we sampled habitat characteristics at 1790 sites used for roosting by 28 radio-marked Mexican Spotted Owls in three study areas in Arizona and New Mexico. We explored potential patterns of variation in roost-site characteristics by estimating similarity among all possible pairs of roost sites and summarizing patterns in these similarity estimates using a linear model. Factors in the model included owl identity and season. We conducted these analyseswithin study areas, because habitat characteristics differed among study areas. We used a repeated-measures model which assumed that similarity estimates computed between roost sites of the same owl or pairs of owls were correlated. This model significantly improved model goodness-of-fit over a null model assuming no such correlation structure. Similarity estimates were relatively high (0.744–0.775) in all three study areas, suggesting consistent patterns of selection among owls within areas. Owl and season effects were relatively small but detectable in all study areas, with the relative magnitude of these effects differing among areas. The seasonal effect was greatest in the area dominated by pine-oak forest and relatively slight in two areas where owls roosted primarily in mixed-conifer forest. Relative to areas where owls roosted in mixed-conifer forest, roosts in pine-oak forest occurred on moderate slopes, on southwest to northwest aspects, and were less concentrated on lower portions of slopes. We suspected that much of this difference reflected differences in stand-development processes in different forest types. This suggested that land managers should incorporate knowledge of such patterns in different forest types and topographic locations in planning decisions involving management of Spotted Owl habitat.

KEY WORDS: *Mexican Spotted Owl;* Strix occidentalis lucida; *Arizona;* New *Mexico; radiotelemetry; repeated measures; roost sites; sources of variation.*

Sitios de perchas de Stnx *occidentalis lucida* marcados con radio-transmisores en Arizona y Nuevo Mexico: fuentes de variabilidad y caracteristicas descriptivas

RESÚMEN.—Para aumentar el conocimiento de los habitats de perchas de *Strix occidentalis lucida* y los factores que influyen en su uso, muestreamos las caracteristicas del habitat en 1790 sitios utilizados como perchas por 28 buhos con radio transmisores en tres areas de estudio en Arizona y Nuevo Mexico. Exploramos los patrones de variación dentro de las caracteristicas mediante la estimación de la similaridad entre todos los posibles pares de sitios de perchas y resumimos los patrones dentro de estos estimativos de similaridad utilizando un modelo linear. Los factores en el modelo incluyeron la identidad de los buhos y la epoca. Condujimos estos análisis dentro de las areas de estudio debido a que las caracteristicas de habitat difirieron entre las areas de estudio. Utilizamos un modelo de repetición de medidas el cual asumio que las estimaciones de similaridad estimadas computados entre los sitios de perchas de las mismas parejas de buhos estaban correlacionadas. Este modelo mejoró significativamente al modelo de bondad de ajuste sobre el modelo nulo, asumiendo la correlación de estructura. Los estimativos de similaridad fueron relativamente altos (0.744–0.775) en las tres areas de estudio, sugiriendo patrones consistentes de selección entre buhos y dentro de las areas. Los efectos de buhos y estacion fueron relativamente pequenos pero detectables en todas las areas de estudio, con una magnitud relativa de estos efectos diferidos entre areas. El efecto de la estacionalidad fue mayor en el area dominada por los bosques de roble y relativamente pequeno en las dos areas en donde los buhos se percharon principalmente en bosques de coniferas mixtas. Con relación a las areas en donde los buhos se perch6 en bosques mixtos de coniferas, las perchas en los bosques de robles y pinos ocurrieron en vertientes moderadas en el suroeste y noroeste, estas fueron menos concentradas en la porción baja de las vertientes. Sospechamos que buena parte de esta diferencia es producto del proceso de desarrollo de arboles en distintos tipos de bosques. Esto sugiere que los planificadores deben incorporar el concimiento de estos patrones en diferentes tipos de bosques y situaciones topográficas en las desiciones de planificacion que involucran el manejo de habitat de los buhos.

[Traduccion de César Márquez]

The Mexican Spotted Owl (*Strix* occidentalis *lucida*) occurs throughout the southwestern United States and northern Mexico in forested mountains and canyonlands (Gutierrez et al. 1995, Ward et al. 1995). It is frequently associated with late-successional forests (Ganey and Dick 1995, GutiCrrez et al. 1995) and was listed as threatened in 1993 because of concerns over loss of forested habitat to timber harvest (Cully and Austin 1993). Previous studies (reviewed in Ganey and Dick 1995) suggest that Mexican Spotted Owls are highly selective in terms of roosting and nesting habitat but forage in a wider array of habitats. Consequently, a recovery plan prepared for the Mexican Spotted Owl (Block et al. 1995) explicitly assumed that availability of roosting/nesting habitat was a key factor limiting the distribution of this owl. Thus, understanding factors underlying use of roosting habitat by Mexican Spotted Owls may be critical to managing habitat for this owl.

Several studies have examined roosting habitat used by Mexican Spotted Owls. Rinkevich and Gutiérrez (1996) and Willey (1998) described roosting habitat in the canyon country of southern Utah. Owls in this region were not closely associated with forests and typically roosted on cliffs near the bottoms of narrow rocky canyons with complex architecture. Johnson (1997) also observed owls associated with steep canyons and roosting on cliffs in Colorado, but most of the roosts he located were in trees. Farther south, owls in Arizona and New Mexico were more closely associated with forests and typically roosted in trees (Ganey and Balda 1989, 1994, Fletcher and Hollis 1994, Zwank et al. 1994, Seamans and GutiCrrez 1995, Hodgson 1996, Stacey and Hodgson 1999). Roost trees were typically located in well-shaded areas, often low on canyon slopes or in canyon bottoms, in relatively cool areas. Similar results have been reported for both Northern (S. o. *caurina,* Thomas et al. 1990) and California (S. o. *occidentalis,* GutiCrrez et al. 1992) Spotted Owls. This may be at least partially due to an aversion to high daytime temperatures during the breeding season (Forsman 1976, Barrows 1981, Ganey et al. 1993, but see Verner et al. 1992).

Several factors limit our understanding of forest roosting habitat of Mexican Spotted Owls. With the exception of Zwank et al. (1994), most information is from the breeding season and does not address potential variation in habitat use between seasons. Most studies have either presented little quantitative information on roost sites (Ganey and Balda 1989), were based on small numbers of owls in limited areas (Ganey and Balda 1994, Zwank et al. 1994, Hodgson 1996, Stacey and Hodgson 1999), or lumped sites from widely-disparate geographic areas or forest types when summarizing roost-site characteristics (Fletcher and Hollis 1994). All of these factors limit our understanding regarding the extent and sources of variability in habitat use by roosting owls.

In conjunction with studies of home-range size and habitat-use patterns of radio-marked Mexican Spotted Owls in Arizona and New Mexico, we sampled habitat characteristics throughout the year at 1790 roost sites. Our objectives were to explore patterns of variation (owls, areas, and seasons) in roost-site characteristics and describe those roost sites by study area and season. In doing so, we hoped to increase understanding of roost-site characteristics in general and of the extent and sources of variability in roost-site characteristics.

STUDY AREAS

We radio-marked Mexican Spotted Owls in three study areas. The Bar-M Canyon study area was located within the Bar-M and Woods Canyon watersheds, Coconino National Forest, approximately 40 km south of Flagstaff, Arizona. The other study areas were selected to represent different habitat situations within the Sacramento Mountains of southcentral New Mexico. The first area (mesic study area) was located along the Rio Penasco drainage, approximately 12 km southeast of Cloudcroft, New Mexico. The second study area (xeric study area) was located in and around the Sixteen Springs drainage, approximately 18 km northeast of Cloudcroft and approximately 30 km from the mesic study area.

Elevation in the Bar-M Canyon study area ranged from 1850–2440 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*) 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 tremuloides*) also occurred throughout the study area and small numbers of narrowleaf cottonwood (*P. angustifolia*) and box elder (*Acer negundo*) occurred in some canyons.

Topography in the Sacramento Mountains was dominated by moderate to steep montane canyons. Elevation in the mesic study area ranged from approximately 2400–2800 m. Many canyon bottoms consisted of meadows, whereas forests dominated canyon slopes and ridgetops. The predominant forest type was a relatively mesic mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and/or white fir (*Abies concolor*). Southwestern white pine (*P. strobiformis*) was prominent in most stands and ponderosa pine and quaking aspen were frequently present. Elevation in the xeric study area ranged from approximately 2000–2500 m. This study area contained a complex mosaic of mesic and xeric forest types. Mixed-conifer forest was restricted to cool microsites such as drainage bottoms and north-facing slopes. Most south-facing slopes and ridgetops were dominated by woodlands of pinyon pine (*P. edulis*) and alligatorbark juniper, sometimes intermixed with ponderosa pine. Other slopes were dominated by ponderosa pine forest, sometimes with a prominent component of Gambel oak.

METHODS

Field Sampling. We sampled habitat characteristics at 1790 diurnal roost sites used by 28 radio-marked owls (12 females and 16 males). All radio-marked owls were ≥1-yr-old. Roost sites were located by homing in on the radio signal until the owl was observed. If the observer moved slowly, it was often possible to locate the owl and sample habitat characteristics without causing the owl to move. When it appeared that the owl might move, sampling of some variables was omitted to minimize disturbance to the owls. This resulted in missing data, as did human errors (e.g., forgetting to bring sampling equipment). These missing data limited the types of analyses we could conduct, but appeared to be randomly distributed and unrelated to factors in analyses. Further details on capture, radio-marking, and tracking of owls are given in Ganey et al. (1999).

Habitat sampling was essentially plotless, but focused on the roost "microsite," including the roost tree and its immediate surroundings. The sampling scale represented a tradeoff between our desire to sample characteristics at the actual site used by the owl (rather than simply in a forest stand or general area used by the owl) and our desire to minimize disturbance to roosting owls. Because it was usually possible to sample the microsite quickly, we suspected that sampling at this scale minimized disturbance to radio-marked owls relative to sampling larger plots.

Methods for sampling habitat characteristics largely followed Solis (1983). We estimated percent slope using a clinometer. Two samples were taken per site, one up and one down-slope, then averaged for an overall estimate. We estimated aspect of the major slope axis using a compass. To estimate percent canopy cover around the roost tree, we used a spherical densiometer to sample canopy cover at a point 5 m from the roost tree in each cardinal direction, then averaged these samples for an overall estimate. Although we use the term canopy cover here, we recognize that the densiometer actually indexes both vertical and horizontal cover, and thus provides a composite measure of both types of cover. For roost trees sampled, we recorded tree species and measured diameter at breast height (dbh) to the nearest cm using a dbh tape. Roost tree and owl perch heights were estimated to the nearest m using a clinometer. We estimated overstory height as the average of the heights of the three overstory trees nearest to the roost tree (sampled with a clinometer). We computed an index of relative roosting height as (owl roost height/roost tree height) × 100.

We also recorded information on forest cover type, roost tree species, and slope position. Cover type assignment was based on a visual assessment of the dominant and co-dominant tree species present. Mixed-conifer forests were dominated by Douglas-fir and/or white fir. Pine-oak forests were dominated by ponderosa pine with Gambel oak co-dominant; pine forests without a prominent oak component were classified as ponderosa pine forest. Forests that did not fit one of the above descriptions were classified as "other."

Slope position was based on a combination of visual assessment in the field and use of topographic maps. Three categories were recognized: upper third of slopes and ridgetops, middle third of slopes, and lower third of slopes and canyon bottoms.

Data Analysis. Potential sources of variation in roost-site characteristics included individuals, sexes, study areas, and seasons. Because of problems with missing data and diverse variable scales and types, we could not use standard multivariate techniques to partition the variance among these potential sources. Consequently, we explored patterns of variation within study areas by estimating similarity among all possible pairs of roost sites within a study area and summarizing patterns in these similarity estimates using a linear model developed by Dyer (1978). Analyses were conducted within study areas because habitats randomly available varied, sometimes greatly, among study areas.

We used Gower's (1971) coefficient (S_{ij}) to estimate similarity. This coefficient measures similarity on a scale ranging from 0 (where all characteristics differ between samples) to 1 (where all characteristics are identical between samples). The coefficient handles both quantitative and categorical variables, deals conservatively with missing data, and is not sensitive to differences in the scale at which variables were measured (Gower 1971). Similarity between roost sites i and j over k variables was estimated as:

$$S_{ij} = \sum (s_{ijk}) / \sum (\delta_{ijk}),$$

where s_{ijk} measures similarity between roost sites i and j over variable k, and δ_{ijk} represents the possibility of comparing variable k between roost sites i and j ($\delta_{ijk} = 0$ when data are missing for either or both roost sites, 1 otherwise). Where $\delta_{ijk} = 0$, we set $s_{ijk} = 0$ (Gower 1971).

Ten habitat variables were included in the similarity estimates. Quantitative variables included percent slope, roost tree dbh, roost tree height, owl perch height, overstory height, canopy cover, and relative owl height. Categorical variables included cover type, position on slope, and roost tree species. For categorical variables, we set $s_{ijk} = 1$ if roost sites i and j agreed for variable k, 0 otherwise (Gower 1971). For continuous variables with values $x_1, x_2, \ldots, x_n$, of variable k over n roost sites, we set $s_{ijk} = 1 - [(x_i - x_j)/R_k]$, where R_k is the range of variable k in the sample.

We computed S_{ij} using a Fortran program. We then used a regression model (Dyer 1978) to estimate the effect of two factors (owl and season) on similarity estimates for all possible pairs of roost sites:

$$S_{ij} = \beta_0 + \beta_1\Delta_{ij}^{\text{owl}} + \beta_2\Delta_{ij}^{\text{season}},$$

where S_{ij} is the similarity estimate for roost sites i and j, and dummy variable $\Delta_{ij}^{\text{owl}} = 0$ if roost sites i and j were from the same owl and 1 if roost sites i and j were from different owls. Similarly, $\Delta_{ij}^{\text{season}} = 0$ if the two roost sites were from the same season and 1 if not. Sex and territory were not included as factors because they were confounded with owl and because both pair members were radio-marked for only 3 of 11 pairs of owls represented in the Sacramento Mountains. We recognized two seasons, breeding (1 March–30 August) and nonbreeding (1 September–28 February).

Because we sampled multiple roost sites for individual owls, and because a given roost site was included in multiple similarity estimates, there was potentially a high degree of correlation among these estimates (Dyer 1978). To account for this correlation among similarity coefficients estimated between two observations on the same owl, or between two observations on the same pair of owls, we used a repeated-measures model (Morrison 1976, Littell et al. 1996) to estimate regression coefficients. This model estimated a separate within-subject variance and correlation for the same owl or same pair of owls For each season. Degrees of freedom for test statistics on regression coefficients were calculated based on the number of individual owls per study area, rather than on the number of roost sites or pairwise comparisons. This is a conservative approach, similar to a Greenhouse-Geisser maximum reduction in degrees of freedom (Morrison 1976:214), designed to address nonindependence of within-owl samples. We used the likelihood ratio test statistic comparing the model with the correlation structure to the null model without correlation structure to assess the improvement in model fit due to incorporating the correlation structure (Littell et al. 1996). Computations were done using SAS PROC MIXED (v 6.12; SAS Institute lnc. 1997).

We were interested in data on aspect of roost sites because some studies have suggested that roost sites are concentrated on north- or east-facing slopes (Fletcher and Hollis 1994, Seamans and Gutiérrez 1995) and previous evidence suggested that owls may select cool microsites (Barrows 1981, Ganey et al. 1993), which may occur mainly on certain aspects. We did not include data on aspect at roost sites in the above analysis, however, because we were not certain how use of circular data would affect similarity estimates. Instead, we analyzed data on roost-site aspect separately, using Oriana for Windows (version 1.01, Kovach Computing Services, Pentraeth, Anglesey, Wales, U.K.). For each individual owl, we estimated the mean slope aspect (***a***, hereafter referred to as mean azimuth) and the angular deviation (s) around the mean azimuth by season. We tested the hypothesis that roost sites of individuals within season were not significantly concentrated around the mean azimuth, using Rayleigh's *z* statistic (Zar 1974). Where this hypothesis was rejected, we tested the hypothesis that mean azimuths of individuals did not differ between seasons using the Watson-Williams test (Zar 1974). This test was conducted separately for each owl.

For each study area and season, we estimated an overall a and s for that study area, using mean azimuths of individual owls as input. We tested the hypothesis that mean azimuths of individuals were not significantly concentrated around the mean azimuth for the study area, using Rayleigh's *z* statistic. We tested the hypothesis that mean azimuths did not differ between seasons within study area, using the Watson-Williams test.

RESULTS AND DISCUSSION

The repeated-measures model, which assumed that pairs of roost sites compared between the same owl or pair of owls within a season were variably correlated, significantly improved model goodness-of-fit over a null model assuming no correlation ($P < 0.0001$). After accounting for the correlation structure inherent in the data, similarity between roost sites was relatively high in all study areas, ranging from **0.744** in the Sacramento Mountains xeric area to **0.775** in the Bar-M Canyon area. The effects of including a different owl or season in comparisons were slight but detectable in all three areas (Table 1).

Because owls often return to the same stand or general area to roost, especially during the breeding season, similarity estimates could be biased high. Arguing against this explanation, however, is the fact that owl and season effects were relatively slight. That is, comparing roost sites between different owls (which use different portions of a study area) or different seasons decreased similarity only slightly. This suggested that similarity estimates were not biased high by repeated use of the same area by individuals. Rather, it suggested that within a study area, roosts sites varied little among owls or between seasons.

The relative magnitude of the effects of owl and season differed among study areas, however. The owl effect was an order of magnitude greater in the mesic area than the season effect. In contrast, this pattern was reversed in the Bar-M Canyon area, and neither effect was pronounced in the xeric area (Table 1). Because at least one study area

Table 1. Regression coefficients for repeated-measures models relating Gower's similarity coefficient between roost sites of radio-marked Mexican Spotted Owls[a] to owl identity and season. Separate models were estimated for each of three study areas in Arizona and New Mexico.

				SACRAMENTO MOUNTAINS, NEW MEXICO					
	BAR-M CANYON, ARIZONA			MESIC STUDY AREA			XERIC STUDY AREA		
EFFECT	β	SE	P	β	SE	P	β	SE	P
Intercept	0.775	0.0013	<0.001	0.746	0.0005	<0.001	0.744	0.0008	<0.001
Owl	−0.012	0.0014	<0.001	−0.011	0.0005	<0.001	−0.007	0.0008	<0.001
Season	−0.041	0.0008	<0.001	−0.001	0.0003	0.014	−0.004	0.0006	<0.001

[a] Number of owls represented by study area = 13 (Bar-M Canyon), 8 (Sacramento Mountains mesic area), and 7 (Sacramento Mountains xeric area). Number of roost sites sampled = 418 (Bar-M Canyon), 831 (Sacramento Mountains mesic area), and 541 (Sacramento Mountains xeric area). Number of pairwise comparisons = 87,153 (Bar-M Canyon), 344,865 (Sacramento Mountains mesic area), and 146,070 (Sacramento Mountains xeric area)

showed a relatively strong seasonal effect on similarity estimates between roost sites and availability of habitat characteristics varied among study areas, we stratified descriptive statistics for roost-site characteristics by study area and season (Tables 2, 3). Examination of roost-site characteristics provided some possible explanations for the observed differences among areas in similarity estimates. For example, several variables (canopy cover, roost tree species, and slope position) showed more seasonal variation in the Bar-M Canyon area than the other study areas, perhaps explaining the greater seasonal effect observed there. Relative to the breeding season, owls in this area roosted less frequently in Gambel oak during the nonbreeding season, and roosted more often in the middle third of slopes (Table 3). They also used roost sites with markedly lower canopy cover than those used during the breeding season (Table 2). We suspected that the reduced use of deciduous Gambel oak could be explained by the fact that it loses most of its foliage during most of the nonbreeding season. Thus, it would provide neither hiding nor thermal cover for roosting owls for much of this season. The shedding of oak leaves may also explain the lower canopy cover observed at nonbreeding-season roosts in this study area. Most of these roost sites were in pine-oak forest (Table 3). Canopy cover should have been uniformly lower in this forest type to the extent that oak foliage no longer con-

Table 2. Descriptive characteristics of roost sites of radio-marked Mexican Spotted Owls[a] in three study areas in Arizona and New Mexico during the breeding and nonbreeding seasons. Shown are means and standard deviations in parentheses.

			SACRAMENTO MOUNTAINS, NEW MEXICO			
	BAR-M CANYON, ARIZONA		MESIC STUDY AREA		XERIC STUDY AREA	
VARIABLE	BREEDING	NONBREEDING	BREEDING	NONBREEDING	BREEDING	NONBREEDING
Slope (%)	18.9 (13.4)	15.9 (10.8)	35.5 (17.6)	32.6 (16.4)	37.2 (16.0)	29.5 (15.9)
Canopy cover (%)	74.0 (17.0)	59.4 (17.5)	76.0 (13.0)	79.7 (11.8)	69.9 (14.0)	70.3 (20.0)
Roost tree dbh (cm)	32.3 (14.2)	31.1 (11.6)	40.0 (17.1)	42.7 (19.2)	28.5 (13.0)	32.3 (14.6)
Roost tree height (m)	15.2 (7.1)	15.5 (5.5)	20.3 (8.8)	20.9 (7.5)	15.1 (5.8)	16.1 (5.8)
Overstory height (m)	22.3 (5.5)	21.0 (5.7)	29.0 (5.2)	27.3 (5.5)	22.3 (5.2)	20.9 (5.6)
Owl perch height (m)	9.5 (5.2)	10.0 (4.2)	8.2 (4.2)	8.9 (4.0)	6.6 (2.6)	6.9 (3.1)
Relative owl height (%)[b]	64.0 (19.5)	65.8 (18.1)	44.5 (19.6)	45.5 (19.6)	46.0 (16.4)	44.1 (16.7)

[a] Number of owls represented by study area = 13 (Bar-M Canyon), 8 (Sacramento Mountains mesic area), and 7 (Sacramento Mountains xeric area). Number of roost sites sampled for breeding and nonbreeding seasons = 148 and 270 (Bar-M Canyon), 467 and 364 (Sacramento Mountains mesic area), and 287 and 254 (Sacramento Mountains xeric area). Sample sizes varied for individual variables due to missing data.

[b] Relative owl height = (owl height/roost tree height) × 100.

Table 3. Summary statistics (% of sites) for categorical variables at roost sites of radio-marked Mexican Spotted Owls on three study areas in Arizona and New Mexico. Sample sizes (in parentheses) differed by variable, and refer to number of roosts for which variable was recorded.

			SACRAMENTO MOUNTAINS, NEW MEXICO			
	BAR-M CANYON, ARIZONA		MESIC STUDY AREA		XERIC STUDY AREA	
	BREEDING	NONBREEDING	BREEDING	NONBREEDING	BREEDING	NONBREEDING
Cover type	(N = 146)	(N = 262)	(N = 467)	(N = 364)	(N = 287)	(N = 254)
Mixed-conifer			97.4	96.4	90.7	82.4
Ponderosa pine	0.7	3.1			2.7	6.1
Pine-oak	99.3	96.9				
Other			2.6	3.6	6.6	11.5
Slope position	(N = 131)	(N = 268)	(N = 467)	(N = 364)	(N = 287)	(N = 254)
Upper third/ridgetop	43.5	36.6	13.7	19.2	17.4	17.9
Middle third	24.4	40.3	28.7	22.5	22.8	17.6
Lower third/canyon bottom	32.1	23.1	57.6	58.2	59.8	64.5
Tree species	(N = 148)	(N = 270)	(N = 462)	(N = 361)	(N = 287)	(N = 254)
Ponderosa pine	63.5	91.1	2.6	4.7	12.8	17.4
Gambel oak	36.5	8.9	14.7	6.6	11.6	8.5
Douglas-fir			32.5	42.7	55.8	53.0
White fir			35.1	33.8	7.3	4.4
Southwestern white pine			10.8	8.6	9.5	13.0
Other			4.3	3.6	3.0	3.7

tributed to overall canopy cover. There did not appear to be a clear ecological reason for the seasonal variation in slope position, unless increased use of mid-slope positions provided thermal advantages. Possible examples here included avoidance of lower temperatures in canyon bottoms, avoidance of higher winds along upper slopes, or owls seeking greater solar insolation (i.e., basking) during cold weather.

Despite the variability among study areas, however, some consistent trends were apparent. For example, owls in all three study areas generally roosted in the middle third of mid-sized trees ($\bar{x}$ dbh = 28.5–40.0 cm; Table 2) that were surrounded by taller trees. Canopy cover at roost sites averaged between 70–80% except for during the nonbreeding season in the Bar-M Canyon study area. With the exception of three variables related to tree size, roost site characteristics appeared quite similar between the two Sacramento Mountains study areas (Tables 2, 3). We suspected that this was largely because, although the areas differed in overall habitat composition, owls in both areas roosted primarily in mixed-conifer forest. Interestingly, those variables related to tree size (roost tree dbh, roost tree height, and overstory height) were more similar between the Bar-M Canyon and Sacramento Mountains xeric areas than between either of those areas and the Sacramento Mountains mesic area (Table 2), possibly indicating convergence in tree use between the two drier study areas.

Slope aspect at roost sites was significantly ($P < 0.05$) concentrated around the mean azimuth for all owls during both seasons in both study areas in the Sacramento Mountains, and for all owls during the breeding season in the Bar-M study area. In contrast, four of 13 owls tested during the nonbreeding season in Bar-M showed no significant orientation. Mean azimuth differed between seasons for two of six owls tested in the mesic study area, two of six in the xeric study area, and six of eight in the Bar-M study area.

Mean azimuths for individual owls were significantly concentrated ($P < 0.05$) around the mean azimuth for each study area and season except for the Bar-M area during the nonbreeding season (Table 4). Mean azimuth differed between seasons in the Bar-M study area ($F_{1,19}$ = 8.60, P = 0.009), but not in the mesic ($F_{1,12}$ = 0.729, P = 0.41) or xeric areas ($F_{1,12}$ = 0.009, P = 0.98). In general,

Table 4. Summary statistics for orientation of roost sites of radio-marked Mexican Spotted Owls in Arizona and New Mexico by study area and season. Statistics based on mean azimuths for roost sites of individual owls within study areas. N = number of owls.

		BREEDING SEASON					NONBREEDING SEASON			
AREA	N	a^a	r^b	s^c	P^d	N	a^a	r^b	s^c	p^d
Mesic	7	84.7	0.72	46.7	0.021	7	105.6	0.77	41.5	0.010
Xeric	6	28.2	0.95	17.5	<0.001	6	28.7	0.93	22.2	0.002
Bar-M	8	318.8	0.78	40.2	0.004	13	236.6	0.47	70.3	0.053

[a] a = mean azimuth (°).

[b] r = length of mean vector.

[c] s = circular standard deviation.

[d] P-values based on Rayleigh's z statistic.

roosts were oriented toward the east in the mesic area and the northeast in the xeric area during both seasons, with a slight shift to the south evident during the nonbreeding season in the mesic area. Roost sites in the Bar-M area were generally oriented toward the northwest during the breeding season and the southwest during the nonbreeding season. Thus, mean aspects were generally similar between seasons in mixed-conifer forest, but shifted to the south in pine-oak forest during the nonbreeding season. Seasonal differences in roost microclimate would thus likely be greatest in the Bar-M Canyon area, where owls not only roosted more on southerly aspects, but also in more open-canopied situations (Table 2) where they could receive more solar insolation.

CONCLUSIONS

Our results suggested that, at the scale sampled, roost-site characteristics were similar both within and among owls within a study area. They further suggested that microsite characteristics were similar between seasons within two study areas where owls roosted primarily in mixed-conifer forest (Sacramento Mountains), but differed more between seasons within a study area where owls roosted primarily in pine-oak forest (Bar-M Canyon). This suggested that mixed-conifer forest provides stable and favorable conditions for owls year-round, whereas owls residing in pine-oak forests are forced to make greater seasonal adjustments in roost-site use. Finally, our results also suggested that microsite characteristics differed among study areas, as might be expected given differences in habitat availability.

Most previous data on roosting habitat of Mexican Spotted Owls has been specific to breeding-season roost sites, and our results add information collected during the nonbreeding season. Our results generally support analyses at coarser spatial scales suggesting that Mexican Spotted Owls roost primarily in mixed-conifer or pine-oak forests with high canopy cover (Ganey and Balda 1989, 1994, Fletcher and Hollis 1994, Zwank et al. 1994, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Hodgson 1996, Ganey et al. 1999). We suspected that the differences observed in use of cover types among areas was attributable to climatic differences and local occurrence of those cover types that provided the types of well-structured, closed-canopied stands favored by Mexican Spotted Owls (e.g., Ganey and Dick 1995, Seamans and Gutiérrez 1995, Grubb et al. 1997).

Results from the Sacramento Mountains study areas also generally agreed with existing results suggesting that owls roost primarily on the lower portions of relatively steep, north- or east-facing slopes (Fletcher and Hollis 1994, Seamans and Gutiérrez 1995). In contrast, owls in the Bar-M study area tended to roost more often on moderate slopes, on west-facing slopes, and on middle and upper portions of slopes. We suspected that this reflected the importance of the oak component to stand structure in the Bar-M Canyon study area. Because Gambel oak can thrive in more open, sunny, and warm conditions (Moir 1993), well-structured stands may develop on more exposed upper slopes in this study area. This suggested that owls seek out appropriate habitat where it exists, that such habitat is not always restricted to steep slopes, canyon bottoms, or north- or east-facing slopes, and that development of well-structured habitat may occur in different locales in different forest

types. This in turn suggested that, where management of Mexican Spotted Owl habitat is an objective, land managers should incorporate knowledge of standdevelopment patterns in different forest types and topographic locations in planning decisions (see also Camp et al. 1997). Finally, managers may also need to consider seasonal patterns in roost-site selection where owls roost in pine-oak forest. Providing conditions suitable for breeding-season roosts, for example, may not adequately provide for the owls' needs during the nonbreeding season.

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