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BREEDING HABITAT OF THE MEXICAN SPOTTED OWL IN THE TULAROSA MOUNTAINS, NEW MEXICO[1]

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Abstract. We studied nest and roost habitat characteristics of Mexican Spotted Owls (*Strix occidentalis lucida*) in the Tularosa Mountains, New Mexico. Owls selected both nesting and roosting sites in mixed-conifer forests that contained an oak (*Quercus* sp.) component more frequently than expected by chance. With the exception of one cliff site, no owls were observed using piñon pine (*Pinus edulis*)/alligator juniper (*Juniperus deppeana*) woodlands for nesting or roosting. Owls selected nest and roost sites in forests characterized by mature (dbh > 45.5 cm) trees with high variation in tree heights and canopy closure >75%. Because we found little difference between nest microsites and their surrounding forest patches, the presence of a suitable nest structure may have determined nest-site selection within nest stands. Characteristics that best described nest sites in the Tularosa Mountains were also applicable to Mexican Spotted Owl nest sites in surrounding mountains. Seventy-five percent ($n = 28$) of nests were in Douglas-fir (*Pseudotsuga menziesii*), and 61% ($n = 28$) of nest structures were on clumps of limbs caused by dwarf mistletoe (*Arceuthobium* sp.) infections. Nest trees averaged 163.7 years of age (SD = 44.8) and 60.6 cm in diameter (SD = 22.4).

Key words: Strix occidentalis lucida; *Mexican Spotted Owl; breeding season habitat; habitat selection; nests; roosts; Tularosa Mountains.*

INTRODUCTION

It has been suggested that the Mexican Spotted Owl (*Strix occidentalis lucida*) is dependent on a narrow range of habitats (USDI 1993). The subspecies was listed as threatened by the U.S. Fish and Wildlife Service because of past and projected habitat loss (USDI 1993). Despite its legal status, few studies of habitat use by the owl have been conducted. Published studies have been limited to either rocky canyon habitat (Rinkevich 1991), which represents less than 10% of Mexican Spotted Owl habitat in the southwestern U.S. (USDI 1993), general surveys (Ganey and Balda 1989a), or studies of a few radio-marked birds (Ganey and Balda 1989b, 1994; Zwank et al. 1994).

We studied nesting and roosting habitat associations of a territorial population of Mexican Spotted Owls occupying a distinct mountain range. Our goal was to describe nest-tree characteristics and test second- and third-order habitat selection (Johnson 1980). Our null hypotheses were: (1) no difference exists between nesting habitat and random habitat distributed throughout the study area; (2) no difference exists between nesting habitat and general habitat within nest stands; and (3) no difference exists between roosting habitat and random habitat distributed throughout the study area.

STUDY AREA AND METHODS

The 323 km² study area encompassed most of the Tularosa Mountains, located eight km northeast of Reserve, New Mexico. The land was managed by the Gila National Forest, USDA Forest Service, primarily for livestock and timber production. Shelterwood and select cutting (Smith 1962) were the predominant logging methods. The climate was characterized by mild summers and cold winters. Elevation ranged from 1,990 to 2,900 m. Most of the study area consisted of forested canyons and mountainsides, with some prairies and mesas.

The three dominant vegetation types present on the study area (Dick-Peddie 1993) were upper montane coniferous forest, lower montane coniferous forest, and coniferous woodland. Upper montane coniferous forests (mixed-conifer) were dominated by Douglas-fir (*Pseudotsuga menziesii*) and sometimes white fir (*Abies concolor*). Also present in the overstory were southwestern white pine (*Pinus strobiformis*), quaking aspen (*Populus tremuloides*), and ponderosa pine (*P. ponderosa*). We divided upper montane coniferous

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forest into pure mixed-conifer (MC), and mixed-conifer/oak (MCO) if Gambel oak (*Quercus gambelii*) was dominant or codominant in the understory (based on a visual assessment). Lower montane forests (pine/oak or PO) were dominated by ponderosa pine in the overstory and Gambel oak in the understory. Coniferous woodlands were dominated by piñon pine (*P. edulis*) and alligator juniper (*Juniperus deppeana*).

OWL SURVEYS

We surveyed the entire study area at least three times each year, 1 April to 20 August, 1991 to 1994, using methods developed by Forsman (1983) and Franklin et al. (1990). We attempted to locate and capture all Spotted Owls within the study area. We determined the sex of owls by voice (Forsman 1983), and the age of owls by plumage characteristics (Forsman 1981, Moen et al. 1991). We captured owls using a noose pole or mist net (Forsman 1983). Upon initial capture, we banded each adult and subadult owl with an aluminum U.S. Fish and Wildlife Service band and a uniquely colored leg band.

We estimated the reproductive and social status of owls following procedures outlined by Forsman (1983). Because Mexican Spotted Owls did not respond as readily to vocal imitations as Northern Spotted Owls (*S. o. caurina*; personal observation), we often located nest sites by finding females and following them to their nests. We located roosts during the daytime. Usually, roosts were used more than once by an owl, and were characterized by regurgitated prey remains and "whitewash" below them. Only roost sites where owls remained stationary upon initial detection were used in analyses. We recorded owl nest and roost locations on U.S. Geologic Survey maps to the nearest 10 m using universal transverse mercator (UTM) coordinates.

NEST- AND ROOST-SITE CHARACTERISTICS

We measured site characteristics at sample plots centered below owl nests and roosts and at random locations in forested habitat. We tested second-order habitat selection by comparing nest and roost plots with random plots located throughout the study area. We tested third-order habitat selection by comparing nest plots with random plots located within nest stands. We did not test third-order selection of roosting habitat because owls tended to roost throughout a stand and we could not be sure of comparing used with unused habitat. We selected random forest plots throughout the study area by generating random UTM coordinates, locating coordinates on the ground, then centering the plot on the nearest tree (roost comparisons), or on the nearest tree $\geq$27.3 cm dbh (diameter at breast height; nest comparisons). The minimum of 27.3 cm was the dbh of the smallest nest tree. We selected random plots within nest stands by measuring a random distance (30–152 m) in a random direction from the nest, then centering the plot on the nearest tree $\geq$27.3 cm dbh. Hereafter, we refer to random plots located throughout the study area as "random plots," and random plots located within nest stands as "stand plots."

Most of our sampling protocol was adopted from Solis (1983) and LaHaye (1988). We marked all sample plots on 1:24,000 scale topographic maps and estimated elevation using an altimeter and topographic maps. We categorized the forest type and slope position (lower, middle or upper third) at each site, and measured 26 habitat characteristics. We present only a description of variables used in analyses. A full description of variables and measurement techniques was presented by Seamans (1994). At each plot center, we estimated slope aspect with a compass, slope angle (%) with a clinometer, and relative canopy closure (%) with a spherical densiometer. We used a variable radius-plot method (Mueller-Dombois and Ellenberg 1974) with a 20 basal-area-factor wedge prism to estimate basal area (m^2ha^{-1}) of medium ($30.5 \leq$ dbh ≤ 45.7 cm) and mature trees (dbh ≥ 45.8 cm). We measured dbh (cm) with a diameter tape, tree height (m) with a clinometer, and counted the number of potential nest trees within each plot. A potential nest tree was any tree in random plots that contained: (1) a cavity with an opening $\geq$ 48 cm on its long axis; (2) an existing raptor nest; or (3) an existing platform > 60 cm in diameter (e.g., a dwarf mistletoe broom). Although subjective, our definition of a potential nest tree was based on characteristics of actual nest trees. We estimated the average maturity index of all tallied standing trees and snags following the classification of Maser et al. (1979). We used the variance of tree heights and variance of tree diameters of all tallied trees in each sample plot as an index of forest structure heterogeneity. We treated these variances as random variables for subsequent tests. We estimated the percent of ground covered by small (2.5 to 30.0 cm diameter) woody debris with a 22.9

m line intercept transect (Mueller-Dombois and Ellenberg 1974). Large woody debris (>30.0 cm diameter) and basal area of hardwoods were not present in enough plots for analysis following our measurement protocol.

We pooled data among years after finding no differences using a series of Kruskall-Wallis ANOVA tests (Zar 1984), with sequential Bonferroni adjustments (Rice 1989). To assure independence of observations, we used only one nest plot per pair of owls or one roost plot per owl. We compared forest types and slope position of owl sites and random sites using chi-square analysis (Zar 1984). We further compared forest types using simultaneous confidence intervals (Neu et al. 1974). We estimated the mean slope aspect of owl nests and roosts using circular statistics (Batschelet 1981), and compared the mean slope aspect of nests and roosts with random sites using a Watson-Williams test (Zar 1984).

We assessed univariate normality of the variables using skewness, kurtosis, and probability plots. We assessed the equality of variances of variables between groups using an *F*-max test (Zar 1984). We used logarithmic and square root transformations (Zar 1984) to normalize variables and equalize variances. For analyses, we only used those variables which approximated a normal distribution and had comparable variances between groups, either before or after transformation.

Before multivariate comparisons, we tested the assumption of homogeneous variance-covariance matrices using Box's test (Stevens 1986), and made a graphical assessment of multivariate normality using methods presented by du Toit et al. (1986). We tested the null hypotheses of no difference in variable means between owl nest and roost plots and random plots using multivariate analysis of variance (MANOVA; Stevens 1986). For the MANOVA, we used Wilks' Lambda to compare linear combinations of variables.

If the MANOVA was significant, we tested individual variables using a series of *t* tests with sequential Bonferroni adjustments. We then used discriminant analysis (DA; Stevens 1986) to model data, estimate which characteristics contributed the most to differences between groups, and to classify an independent sample of 13 nests from different areas. Seven nests were in the White Mountains, Arizona. Five nests were in the San Francisco Mountains, and one nest in the Pinos Altos Range, New Mexico. We estimated the relative importance of variables by the magnitude of their structure coefficients (Stevens 1986). We used cross validation (Capen et al. 1986) to evaluate DA model stability. For the cross validation, we withheld a random subsample of 25% of the plots and then classified these plots using the discriminant function derived from the remaining plots. We repeated this process 20 times, with replacement each time, for each comparison. We calculated chance corrected classification rates using Cohen's Kappa statistic (Titus et al. 1984).

NEST-TREE CHARACTERISTICS

We took detailed measurements of all nest trees using the same techniques used for measuring trees in sample plots. We used circular statistics to estimate mean orientation of the nest relative to the tree trunk, and Rayleigh's test (Batschelet 1981) to estimate if the mean orientation differed from a random distribution. We used a chi-square analysis to test the null hypothesis that tree species distribution did not differ between actual and potential nest tree distributions.

We estimated nest-tree age by extracting a core sample with an increment borer and counting the rings. If we did not reach the pith, we used the count of visible rings as a minimum estimate of age. As with plots, we used only one nest per pair of owls to estimate nest-tree characteristics to assure independence of observations. We randomly selected one nest if a pair of owls used different nests in different years. We used paired-sample *t* tests (Zar 1984) with a sequential Bonferroni adjustment to compare nest tree height, dbh, and age to a random tree within the nest stand. Random trees were located by walking a random distance (30–152 m) in a random direction from the nest tree.

RESULTS

ROOST-SITE CHARACTERISTICS

Of 157 roost sites we measured, we used 79 (one each for 41 males and 38 females) as independent samples for analysis. The distribution of forest types at Spotted Owl roosts differed from random sites throughout the study area ($\chi^2 = 62.66$, df = 3, $P < 0.001$), with most roosts in the mixed-conifer/oak forest type (Fig. 1). Roosts were located between 2,150 m and 2,800 m elevation.

TABLE 1. Habitat characteristics at Mexican Spotted Owl roost (n = 78) and random plots (n = 71) in the Tularosa Mountains, New Mexico, 1991–1994.

Variable	Means (SD) Roost	Means (SD) Random[b]	t[c]	Discriminant analysis: Cross-validation[a] Mean rank	Cross-validation[a] Mean structure coefficient[d]	Pooled data structure coefficient
Canopy closure (%)	85.2 (9.9)	50.6 (22.4)	12.07*	1.0	0.806	0.828
Tree height (m)	19.0 (4.3)	11.9 (5.4)	8.76*	2.4	0.586	0.588
Tree height variance	2.2 (1.4)	1.1 (1.0)	8.48*	2.7	0.564	0.577
Live tree BA (m^2 ha^{-1})	31.7 (14.2)	19.8 (11.8)	5.96*	5.2	0.395	0.405
Mature tree BA (m^2 ha^{-1})[e]	9.0 (7.9)	3.7 (5.6)	5.93*	5.4	0.378	0.378
Slope angle (%)	18.2 (8.4)	11.4 (5.8)	5.96*	6.1	0.366	0.375
Small debris cover (%)[f]	4.2 (3.5)	1.9 (2.4)	5.36*	6.7	0.359	0.360
Tree dbh variance	6.4 (3.9)	5.0 (4.9)	5.08*	6.7	0.345	0.348
Tree dbh (cm)	35.6 (10.8)	31.0 (11.2)	2.52*	9.1	0.172	0.169
Medium tree BA (m^2 ha^{-1})[g]	8.4 (8.2)	6.1 (6.5)	1.41	9.9	0.092	0.095

[a] Discriminant analysis results for 20 cross-validations.
[b] Random sites located throughout study area.
[c] t values (df = 146), * significant at α = 0.05 with Bonferroni simultaneous confidence intervals ($P_i \leq \alpha/(1 + k - i)$).
[d] Structure coefficient is correlation between a single variable and discriminant function.
[e] Basal area of mature trees (dbh ≥ 45.8 cm).
[f] Percent of ground covered by small woody debris (≥2.5 cm and ≤30.0 cm diameter at large end).
[g] Basal area of medium trees (30.5 ≤ dbh ≤ 45.7 cm).

Position of roost sites on the slope differed from a random distribution (χ^2 = 39.92, df = 2, P < 0.001). Sixty-four roosts (81%) were located on the lower third of the slope, 13 (16%) on the middle third, and two (3%) on the upper third. Mean slope aspect at roost sites was northerly (mean aspect = 4.6°, mean vector length = 0.50, angular deviation = 62.7°), but was not different from random sites (F = 2.30, df = 1, 148, P = 0.132). We did not use one roost site for further analysis because it was on a cliff ledge and forest characteristics could not be estimated (thus, n = 78 for further tests).

Characteristics of 78 roost and 71 random plots approximated a multivariate normal distribution, but had heterogenous variance-covariance matrices (Box's test, F = 2.534, P < 0.001). Roost plots differed from random plots (MANOVA; Wilks' Lambda = 0.39, F = 20.84, df = 10, 137, P < 0.001). The mean value for each variable was greater for roost than random plots (Table 1). The t tests indicated all variables were different between roost and random plots, except basal area of medium trees (Table 1). Higher canopy closure, taller trees and greater variation in tree heights best separated roosts from random plots in the DA (Table 1). The similarity of structure coefficients between the pooled DA and cross-validations indicated the results were stable. The pooled DA correctly classified 89.9% (133) of the roost and random plots (significantly better than chance; Cohen's Kappa = 0.797, P < 0.001). Of the plots withheld in the cross-validations, 86.4% were correctly classified by the resulting DAs (significantly better than chance; Cohen's Kappa = 0.727, P < 0.001).

NEST-SITE CHARACTERISTICS

Of 49 nest sites measured, we used 28 as independent samples for analysis. These sites represented 28 different breeding pairs. The distribution of forest types at nests differed from random sites (χ^2 = 30.78, df = 3, P < 0.001), with most nests in the mixed-conifer/oak forest type (Fig. 1). Nests were located between 2,190 m and 2,715 m elevation. Position of nest sites on the slope differed from a random distribution (χ^2 = 9.38, df = 2, P = 0.009). Twenty nests (74%) were located on the lower third of the slope, six (22%) on the middle third, and one (4%) on the upper third. Mean slope aspect at nest sites was northerly (mean aspect = 336.4°, mean vector length = 0.48, angular deviation = 59.5°), and differed from random sites (F = 54.14, df = 1, 54, P < 0.001).

We did not use one nest site for further analysis because it was on a cliff ledge and forest characteristics could not be estimated (thus, n = 27 for further tests). We measured habitat characteristics at 27 random plots located throughout the study area for comparison. Including nest trees, we estimated that almost nine times as many potential nest trees existed in 27 nest plots ($\bar{x}$ = 1.33, SD = 0.68) as in 27 stand plots ($\bar{x}$ =

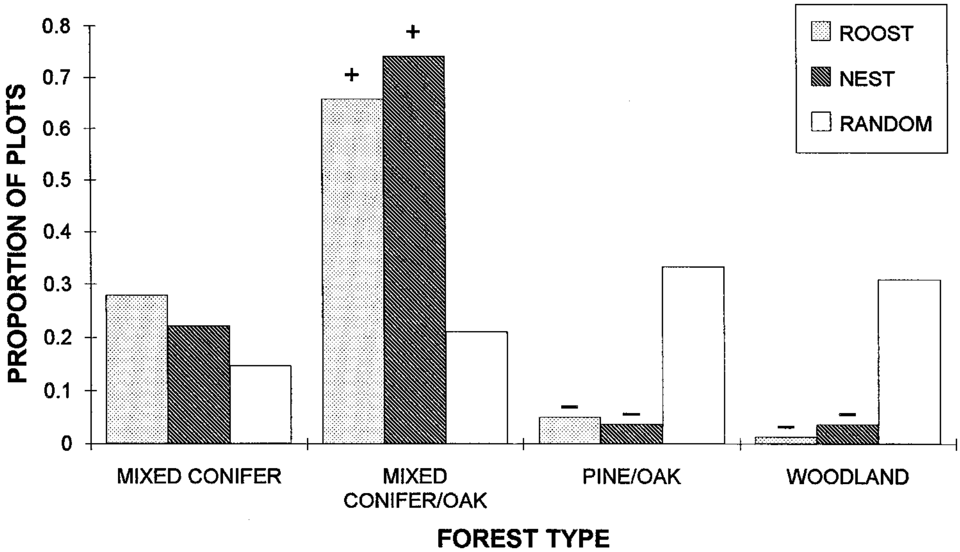

FIGURE 1. Distribution of forest types at Mexican Spotted Owl nests (n = 28), roosts (n = 79), and at random sites located throughout the study area (n = 98), in the Tularosa Mountains, New Mexico, 1991–1994. For forest types at nests and roosts: "–" indicates used less than expected; "+" indicates used more than expected; and no sign indicates used equal to expected. Expected values based on relative availability of forest types.

0.15, SD = 0.46). We located no potential nest trees in random plots.

Characteristics of 27 nest and 27 random plots approximated a multivariate normal distribution, but had heterogenous variance-covariance matrices (Box's test, $F = 2.00$, $P < 0.001$). Nest plots differed from random plots (MANOVA; Wilks' Lambda = 0.52, $F = 3.98$, df = 10, 43, $P = 0.001$). The t tests indicated five of the 10 variables differed between nest and random plots (Table 2). Greater variation in tree heights, taller trees, higher canopy closure and greater basal area of mature trees best separated nest from random sites in the DA (Table 2). The similarity of structure coefficients between the pooled DA and the cross-validations indicated the results were stable. The pooled DA correctly classified 77.8% (42) of the nest and random sites (significantly better than chance; Cohen's Kappa = 0.556, $P < 0.001$). Of the plots withheld in the cross-validations, 70.5% were correctly classified by the resulting DAs (significantly better than chance; Cohen's Kappa = 0.416, $P < 0.001$). The pooled DA correctly classified 84.6% (11) of the nest sites measured from different mountain ranges, and 88.1% (13 samples in 20 cross-validations) were correctly classified by the cross-validation DAs.

Characteristics of 27 nest and 27 stand plots approximated a multivariate normal distribution, and had similar variance-covariance matrices (Box's test, $F = 1.34$, $P = 0.050$). Nest plots did not differ from stand plots (Wilks' Lambda = 0.80, $F = 1.10$, df = 10, 43, $P = 0.381$).

NEST-TREE CHARACTERISTICS

Twenty-eight different nesting pairs of Mexican Spotted Owls used 49 different nests during the study. One nest was used all four years, one nest was used three years, ten nests were used two years, and 37 nests were used for one year. Spotted Owls used six nest structure types. Seventeen (61%) were on clumps of limbs deformed by dwarf mistletoe infections, three (10.5%) were old squirrel nests, three (10.5%) were old raptor nests, two (7%) were natural accumulations of debris (conifer needles, leaves, and limbs) on branches, two (7%) were tree cavities, and one (4%) was a cliff ledge. All nests on limbs deformed by dwarf mistletoe infection were in Douglas-fir. At least 12 other sites on the study area had cliffs similar in character to the actual nest, but none were used by owls. Mean aspect of nests relative to the tree trunk was north-easterly (mean aspect = 61.2°, mean vector length = 0.49, angular de-

TABLE 2. Habitat characteristics at Mexican Spotted Owl nest ($n = 27$) and random plots ($n = 27$) in the Tularosa Mountains, New Mexico, 1991–1994.

Variable	Means (SD)			Discriminant analysis		
				Cross-validation[a]		
	Nest	Random[b]	t^c	Mean rank	Mean structure coefficient[d]	Pooled data structure coefficient
Tree height variance	2.2 (1.0)	1.1 (1.0)	5.20*	1.4	0.690	0.750
Mature tree BA (m^2 ha^{-1})[e]	12.4 (10.5)	4.3 (6.0)	4.38*	3.1	0.571	0.631
Tree height (m)	20.4 (5.8)	13.9 (5.7)	4.16*	3.1	0.565	0.599
Canopy closure (%)	75.9 (14.1)	56.3 (20.4)	4.13*	3.1	0.558	0.595
Tree dbh variance	8.3 (7.0)	5.8 (4.5)	3.15*	5.2	0.426	0.454
Small debris cover (%)[f]	3.3 (2.4)	2.2 (3.2)	2.41	6.5	0.333	0.347
Live tree BA (m^2 ha^{-1})	25.3 (13.2)	18.9 (10.8)	2.34	6.9	0.323	0.337
Tree dbh (cm)	44.7 (10.7)	38.6 (12.3)	1.98	7.7	0.250	0.285
Slope angle (%)	15.7 (7.4)	13.0 (7.6)	1.30	8.3	0.196	0.188
Medium tree BA (m^2 ha^{-1})[g]	8.3 (7.0)	8.5 (6.5)	0.13	9.9	0.052	0.019

[a] Discriminant analysis results for 20 cross-validations.
[b] Random sites located throughout study area.
[c] t values (df = 52), * significant at $\alpha = 0.05$ with Bonferroni simultaneous confidence intervals ($P_i \leq \alpha/(1 + k - i)$).
[d] Structure coefficient is correlation between a single variable and discriminant function.
[e] Basal area of mature trees (dbh $\geq$ 45.8 cm).
[f] Percent of ground covered by small woody debris ($\geq$2.5 cm and $\leq$30.0 cm diameter at large end).
[g] Basal area of medium trees (30.5 $\leq$ dbh $\leq$ 45.7 cm).

viation = 22.3°), which differed from a random distribution ($z = 22.28$, $P < 0.001$).

Seventy-eight percent (21) of nest trees were Douglas-fir, 11% (3) were white fir, 7% (2) were ponderosa pine, and 4% (1) were southwestern white pine. The distribution of potential nest tree species ($n = 52$) did not differ from actual nest tree species ($\chi^2 = 4.96$, df = 3, $P = 0.175$). Nest trees were older, larger, and taller than trees randomly located within the nest stand (Table 3). Only one nest tree, a southwestern white pine, was dead.

DISCUSSION

Most Mexican Spotted Owl nest and roost sites were found on the lower third of north-facing slopes. This corresponded to the distribution of mature mixed-conifer forests on the study area. In addition, most nest and roost sites had an understory of Gambel oak, which added to the forest structure. Both Northern and California Spotted Owls (*S. o. occidentalis*) have shown some selection for nest and roost sites on the lower portions of slopes, but slope orientation patterns were not always consistent (LaHaye 1988, Blakesley et al. 1992, Gutiérrez et al. 1992, Buchanan et al. 1993, Folliard 1993). This was probably because nesting and roosting habitat was more broadly distributed in the more temperate forest areas, and not limited to north-facing slopes.

Patterns of habitat use by individual Mexican Spotted Owls (Kertell 1977, Ganey and Balda 1989a, Rinkevich 1991, Ganey and Balda 1994)

TABLE 3. Characteristics of Mexican Spotted Owl nest ($n = 27$) and random trees ($n = 27$) in the Tularosa Mountains, New Mexico, 1991–1994.

Variable	Nest trees		Random trees[a]		
	$\bar{x}$	SD	$\bar{x}$	SD	t^b
Age (yrs.)	163.6	44.8[c]	119.6	64.6	3.92*
Tree height (m)	27.2	6.5	18.2	8.6	3.81*
Dbh (cm)	60.6	22.4	43.1	25.4	3.26*
Maturity index[d]	1.3	0.5	1.5	1.2	0.69
Nest height (m)	15.0	4.9	—	—	—

[a] Random trees were located a random distance (30–152 m) in a random direction from the nest tree.
[b] t values from matched pair test (df = 2,26 except for age where df = 2,23). * significant at $\alpha = 0.05$ with Bonferroni simultaneous confidence intervals ($P_i \leq \alpha/(1 + k - i)$).
[c] Age could not be accurately estimated for one tree due to its size. An estimated 71% of the 61.5 cm radius was extracted, and 186 rings were counted.
[d] Maturity index of trees based on Maser et al. (1979).

was corroborated by our study. Although the Mexican Spotted Owl probably has been isolated from the two coastal subspecies for thousands of years, and may possibly represent a separate species (Barrowclough and Gutiérrez 1990), habitat selection among the three subspecies was similar (Forsman et al. 1984, LaHaye 1988, Carey et al. 1992, Gutiérrez et al. 1992). The main difference between the Mexican and coastal subspecies was that average tree size in Mexican Spotted Owl habitat was smaller. Thus, all three subspecies selected nest and roost sites that exhibited complex vegetation structure (high canopy closure, high variation in tree heights and diameters, and multiple canopy layers). Among all three subspecies, mature mixed-conifer forests frequently provided this multi-storied habitat.

In our study, owls selected nest and roost sites primarily in mixed-conifer forest with larger and taller trees, higher canopy closure, and higher variation in tree heights than random sites. These characteristics were indicative of late successional forests in the southwestern United States (Mehl 1992, Moir 1992). Habitats such as piñon-juniper woodland or even-aged pine and mixed-conifer stands lacked the vertical structure typical of nest and roost sites. Our habitat model successfully classified nests outside the study area as well as nests inside the area, suggesting that the characteristics we found important in describing owl habitat were regionally applicable.

We found little difference between actual nest sites and the stands in which they occurred. This indicated owls may have selected nest sites surrounded by mature mixed-conifer forest, and that selection of a particular nest site within a nest stand was partially due to the presence of a tree with a suitable nest structure. Thus, management for Spotted Owl nest sites should also include the surrounding stand of timber.

Approximately 10% of our nest and roost sites had been partially logged in the past. With the exception of one nest site (logged 10 years ago), most of these stands were selectively logged more than 40 years ago. This harvest method left many residual trees, as well as trees in younger age classes, resulting in uneven-aged stands similar in character to the unlogged stands. The use of partially logged forests by owls has also been documented for both the Northern and California Spotted Owl (Forsman et al. 1977, Verner et al. 1992, Buchanan et al. 1993, Folliard 1993).

Forests composed of larger trees with high variation in tree heights may provide an accessible prey base for Spotted Owls and provide protection from potential predators such as Great Horned Owls (*Bubo virginianus*; Forsman et al. 1984, Carey 1985, Gutiérrez 1985). In addition, Spotted Owls are heat intolerant and may require mature, multi-storied forests or deep, rock-walled canyons for thermoregulation (Barrows 1981, Forsman et al. 1984, Carey 1985, Gutiérrez 1985, Carey et al. 1992, Ganey et al. 1993). The lower portion of north-facing slopes, forested with multi-storied mixed-conifer habitat, may have provided suitable microclimates for owls.

Spotted Owls do not build their own nests, but rely on the presence of a suitable structure. The presence of a suitable nest structure may be a factor in the selection of territories by Spotted Owls (Carey 1985, Gutiérrez 1985, Forsman et al. 1984). In the population we studied, the predominant use of Douglas-fir nest trees probably was related to the presence of suitable nest structures, primarily dwarf mistletoe brooms. Heavy dwarf mistletoe infections, such as those that resulted in clumps of deformed limbs used as nests, are associated with mature, uncut Douglas-fir forests in the southwestern U.S. (Mathiasen et al. 1990). Excluding actual nest trees, most potential nests were also in Douglas-fir. We located no potential nests in piñon pines or junipers, and few in ponderosa pines. Douglas-fir also has been documented as a primary nest tree for the Northern Spotted Owl (Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993), whereas nest tree selection varied widely in the California Spotted Owl (Gutiérrez et al. 1992).

We found most owls using platform structures for nests, possibly because few trees were large enough to possess suitable cavities. Nest structure type used by Northern and California Spotted Owls was variable. Use of cavities by Northern Spotted Owls dominated some nest samples (Forsman et al. 1984, LaHaye 1988), while platform nests were used in other samples (Buchanan et al. 1993, Folliard 1993). Use of cavities by California Spotted Owls varied by region (Gutiérrez et al. 1992). Thus, these subspecies appeared not to be dependent on a single type of nest structure.

Our results and inferences apply only to forest stands used by Mexican Spotted Owls for nesting and roosting. Mexican and California Spotted Owl foraging habitat tended to be more variable than either nesting or roosting habitat (Gutiérrez et al. 1992, Ganey and Balda 1994). The results of our analyses do not necessarily describe selection by owls for the characteristics we measured (e.g., see James and McCulloch 1990). However, our study supports the generalization that Spotted Owls are habitat specialists (Gutiérrez et al. 1992). In areas occupied by Mexican Spotted Owls where selective logging had occurred, much of the habitat still resembled unlogged forests in structural diversity. Areas that had been repeatedly logged resulted in stands with low height and diameter diversity that were not used by owls for roosting or nesting. Therefore, our findings support the concern that the trend toward even-aged forest management in the southwestern U.S. would be detrimental to the owl (USDI 1993). Alternatively, prudent logging using selective harvest methods with retention of large trees and oaks may hold promise for maintaining Spotted Owl habitat in the Southwest.

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