Habitat Relations



Nesting Habitat of Mexican Spotted Owls in the Sacramento Mountains, New Mexico

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ABSTRACT Understanding the habitat relationships of rare species is critical to conserving populations and habitats of those species. Nesting habitat is suspected to limit distribution of the threatened Mexican spotted owl (Strix occidentalis lucida), and may vary among geographic regions. We studied selection of nesting habitat by Mexican spotted owls within their home ranges in the Sacramento Mountains, New Mexico. We compared characteristics of owl nest trees and nest sites to characteristics of randomly located trees and sites at 2 spatial scales: the general nest vicinity and within activity centers used by spotted owls. Owls nested primarily in mixed-conifer forest (92%), and most nested in cavities in trees or snags (48%), or in dwarf mistletoe (Arceuthobium spp.) witches' brooms (36%). Owl nest trees had greater levels of dwarf mistletoe infection and were larger in diameter than random trees at both of the evaluated spatial scales. Nest trees also were more likely than random trees to be in white fir (Abies concolor) or Douglas-fir (Pseudotsuga menziesii), and in trees or snags with broken tops. Differences between owl nest sites and random sites differed with the scale at which we selected random sites, but at both scales examined, owl nest sites had greater canopy cover and more basal area contributed by large trees and white fir than random sites. In addition, most nest sites occurred in drainage bottoms or on the lower 2 thirds of north- or east-facing slopes. Conservation of owl nesting habitat in this area will require retaining forest patches with high canopy cover and large trees containing cavities or large dwarf mistletoe witches' brooms. Locating forest management treatments on ridgetops or the upper third of slopes and/or on south- or west-facing slopes may reduce impacts to owl nesting habitat while simultaneously targeting the drier forest types most in need of restoration. © 2013 The Wildlife Society.

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Understanding habitat requirements is fundamental to conserving or recovering populations of rare species. The Mexican spotted owl (*Strix occidentalis lucida*) is a federally listed threatened species whose recovery is tightly linked to conservation of nesting habitat (United States Department of the Interior Fish and Wildlife Service [USDI FWS] 2012). This owl occurs in the southwestern United States

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⁵Present address: U.S. Fish & Wildlife Service, National Wildlife Refuge System, Inventory and Monitoring Branch, Fort Collins, CO, USA and portions of Mexico, typically residing either in montane conifer forests or incised rocky canyons (Gutiérrez et al. 1995, Ward et al. 1995). A recovery plan and a recent revision developed for this owl (USDI FWS 1995, 2012) identified nesting habitat as the primary factor limiting the owl's distribution. Management recommendations within these plans focused on retaining and developing forest habitat for use by nesting owls.

Despite this emphasis on nesting habitat, published studies on nesting habitat used by Mexican spotted owls are restricted to 2 study areas in the Upper Gila Mountains Ecological Management Unit, 1 of 5 such geographic subdivisions recognized within the United States range of this owl (USDI FWS 2012). These studies examined both landscape composition around owl nests (Peery et al. 1999, May and Gutiérrez 2002) and structural features of forested nest sites (Seamans and Gutiérrez 1995, May et al. 2004). They evaluated habitat selection (Johnson 1980) by contrasting areas used by owls with randomly located areas within large study areas. Within both study areas, owls selected for mixedconifer forest and areas around owl nests contained greater amounts of mature forest or younger forests with high canopy cover and residual large trees than random areas (Peery et al. 1999, May and Gutiérrez 2002). Nest sites in both study areas featured greater canopy cover and basal area of large trees than random sites, and were more likely to be located on lower portions of slopes and on northerly aspects (Seamans and Gutiérrez 1995, May et al. 2004).

Ecological variability is pronounced within the range of the Mexican spotted owl (USDI FWS 2012), and patterns of habitat use differ across that range (Ganey and Dick 1995). Consequently, understanding nesting habitat requirements requires information from across that range. We studied nesting habitat of Mexican spotted owls in the Sacramento Mountains, south-central New Mexico, in an area lacking previous published studies of nesting habitat. The Sacramento Mountains occur within the Basin and Range-East Ecological Management Unit and contain the bulk of the population of Mexican spotted owls within that Ecological Management Unit (Ward et al. 1995, USDI FWS 2012). This population is relatively isolated genetically from larger populations elsewhere within the owl's range (Barrowclough et al. 2006). Consequently, the viability of this population likely depends on internal population dynamics, suggesting that managers should maintain sufficient habitat to allow dynamic processes to favor Mexican spotted owls (Barrowclough et al. 2006:198). Our study was designed to aid managers charged with conserving owl habitat by providing information on nesting habitat selection within owl home ranges in this region (third-order habitat selection, sensu Johnson 1980). Specific objectives included 1) describing nest trees and structures used by Mexican spotted owls, 2) quantifying forest structural attributes at owl nest sites, and 3) comparing attributes of nest trees and nest sites to those of randomly located trees and sites at 2 spatial scales.

STUDY AREA

We conducted this study within the Sacramento Mountains of south-central New Mexico, within the Sacramento Ranger District, Lincoln National Forest. This range is a large montane island surrounded by a desert and semi-desert matrix (Kaufmann et al. 1998). Elevation ranged from 2,130 m to 2,980 m within the study area. Precipitation averaged 65 cm/year at Cloudcroft, New Mexico (within the study area, elevation 2,652 m) with summer thunderstorms providing more than 60% of annual precipitation and most of the remainder occurring as winter snowfall (Kaufmann et al. 1998).

Most of our study area occurred at higher elevations near the crest of the southern Sacramento Mountains. Montane canyons dominated topography, with forests on most canyon slopes and ridgetops and a mix of forests and montane meadows common in canyon bottoms. Mixed-conifer forest, dominated by white fir (*Abies concolor*) and/or Douglas-fir (*Pseudotsuga menziesii*), was the primary forest type in the study area. Southwestern white pine (*Pinus strobiformis*) was prominent in some forest patches, and quaking aspen (*Populus tremuloides*) was relatively common. Ponderosa pine (*Pinus ponderosa*) was uncommon in many patches, occurring mainly in drier sites. Blue (*Picea pungens*) and Engelmann (*Picea engelmannii*) spruce occurred in some areas. Maples (*Acer* spp.) were common in the understory at some sites, and the most common shrub species was oceanspray (*Holodiscus dumosus*).

The northeastern and eastern portions of the study area, as well as some lower elevation areas, were dominated by drier forest types. Here, mixed-conifer forest was restricted to cooler microsites such as drainage bottoms and north-facing slopes, and these patches were dominated by Douglas-fir and ponderosa pine with lesser amounts of white fir. Woodlands of piñon pine (*P. edulis*) and alligator juniper (*Juniperus deppeana*) dominated most ridgetops and south-facing slopes. Other slopes were dominated by ponderosa pine forest, sometimes with a prominent component of Gambel oak (*Quercus gambelii*). Gray oak (*Quercus griseus*) and wavyleaf oak (*Quercus undulatus*) also were present in some areas.

The Sacramento Mountains feature a long growing season, fertile soils, and productive montane forests. Major natural disturbance agents structuring these forests historically included fire and insect outbreaks. Since approximately 1880, forest structure has been intensively influenced by human activities, including logging, fire suppression, livestock grazing, housing developments, and farming within montane meadows. Logging was relatively pervasive in the Sacramento Mountains from the late 1800s through approximately 1940, and continues at lower levels today. As a result of the combined effects of logging, livestock grazing, and fire suppression, the forest today is more homogeneous in terms of size, age, and patch structure than the forests preceding these activities, and <5% of mixedconifer forest area today is in an old-growth condition versus an estimated 10-26% in 1880 (Kaufmann et al. 1998:70-71).

METHODS

Sampling Design

Previous studies of nesting habitat of Mexican spotted owls evaluated both second- and third-order habitat selection as defined by Johnson (1980), but their primary focus was on second-order selection. Because these studies selected random sites within large study areas, many of the sites used to evaluate second-order selection likely occurred far from areas used by territorial owls, and in forest types not typically used by owls. For example, approximately 95% of nest sites sampled by Seamans and Gutiérrez (1995: Fig. 2) occurred in mixed-conifer forest, yet approximately 65-70% of their random sites occurred in ponderosa pine and pinyonjuniper woodland. May et al. (2004) did not provide data on forest types at random sites. However, mixed-conifer forest comprised only 5% of their study area, yet contained 38% of located nests, suggesting that a similar mismatch between owl nest sites and random sites may have occurred in their study area. Because forest structural characteristics differ naturally among forest types, researchers have difficulty

determining whether observed differences reflect selection for or against particular forest characteristics, or are driven primarily by differences among forest types.

To avoid this difficulty, we focused on third-order habitat selection and restricted our sample of random sites to spatial areas and forest types used by owls. To achieve this, we selected all random plots from within a 201-ha area around the nest. This area was approximately 80% of the recommended size (243 ha) for Protected Activity Centers (PACs) designated for territorial owls following USDI FWS (1995, 2012). That recommendation for PAC size was based on the estimated size of activity centers of radio-marked pairs of owls (USDI FWS 1995, 2012), which were known to be both considerably smaller than owl home ranges and heavily used by resident owls (Ganey and Dick 1995). Consequently, we are confident that our sampled area was within the home ranges of resident owls, likely within their activity centers, and therefore available for use by owls. This 201-ha area also represented the only scale at which vegetation composition differed significantly between owl and random areas in an Arizona study area (May and Gutiérrez 2002), and examination of Figures 1 and 2 in Peery et al. (1999) suggests that differences between owl and random landscapes also were greatest at approximately this scale in their New Mexico study area. This area thus should be dominated by the forest types that owls use.

Within this area, we measured tree and forest structural attributes in matched sets of circular plots, with each set consisting of a plot around an owl nest site and 2 plots randomly located at varying distances from that nest. We centered nest site plots on a nest tree used at least once by spotted owls between 1996 and 2011. Owl demography survey crews located all nest sites using standard techniques (Forsman 1983, Franklin et al. 1996). We centered all other plots on the closest tree \geq 25 cm diameter at breast height (dbh) to a randomly generated Universal Transverse Mercator (UTM) coordinate pair. We chose the 25-cm minimum diameter for random center trees to approximate the diameter of the smallest nest tree sampled in another study area (27 cm; Seamans and Gutiérrez 1995), and to minimize any potential bias caused by centering nest site plots on large trees and centering other plots on smaller trees or on treeless areas that could not be used for nesting (Gutiérrez et al. 1992:83). Nest vicinity plots were located at randomly generated points within 200 m of the matched nest tree (area included = 12.6 ha), with the constraint that resulting plots could not overlap spatially with nest site plots. These plots represented conditions in the general vicinity of nest sites. We intended PAC plots to sample areas within activity centers of resident owls, but outside of the immediate nest vicinity. These plots were located at randomly located points 200-800 m from the nest tree. Thus, all random plots were spatially matched with a specific nest site plot, and were selected from within an area expected to receive concentrated use by owls and dominated by the forest types used by owls. Consequently, any observed differences between nest sites and random sites are unlikely to be due to random variation among forest types.

Data Collection

Nest and random trees.-For each nest tree, and for center trees on other plots, we recorded tree species, dbh (nearest cm, measured with a dbh tape), height (nearest m, measured with a clinometer), condition (live or dead), and top type (intact or broken). Mexican spotted owls sometimes nest in witches' brooms (Seamans and Gutiérrez 1995, Ganey et al. 2011), defined here as debris platforms formed where a dense mass of shoots originates from a dwarf mistletoe (Arceuthobium spp., most likely A. douglassii) infection. Consequently, we also estimated broom volume rating (BVR), an index of dwarf mistletoe infection level. The BVR rates infection levels based on the volume of each crown third occupied by mistletoe brooms (Tinnin 1998). We recorded BVR for each crown third as 0 (no brooms present), 1 (≤50% broom coverage), or 2 (>50% broom coverage), then summed these values to generate an estimate of BVR for the entire tree.

For nest trees, we also recorded nest type (dwarf mistletoe broom, other platform, cavity in broken top tree or snag, cavity in the side of a tree or snag, or unknown), and nest height (nearest m). For nests in broken-topped trees, we recorded the presence or absence of a secondary top, formed when a lateral limb grew up to overtop the broken top, providing shade and shelter. For nests in dwarf mistletoe brooms, we categorized brooms using a system that classifies brooms into 3 types based on their structure and point of origin on the host tree (Tinnin and Knutson 1985; see Parks et al. 1999: Fig. 1 for depictions of broom types). Type I brooms originate near the distal ends of branches, and are limited in size by their weight. Type II brooms originate within a few feet of the bole. The supporting limb is greatly thickened and often turns upward. Type III brooms originate on the bole, and have a dense profusion of branches. Because we did not climb nest trees, distinguishing between type II and III brooms was sometimes difficult. Consequently, we included a fourth category for brooms that were either type II or type III, but for which we could not determine exact broom type.

Nest and random plots.—We measured forest structural attributes in nested circular plots. We counted and measured larger trees and snags (dbh >30 cm) within a 0.1-ha plot, and small trees and snags (dbh \geq 10 cm and \leq 30 cm), which were more abundant, within a 0.03-ha plot. We recorded species and dbh of all trees and snags within the plots. We measured all logs \geq 20 cm in large-end diameter and \geq 1 m in length within the 0.03-ha plot discussed above. For each log, we recorded length within the plot (nearest 0.1 m) and mean diameter (nearest cm) of the portion within the plot.

We estimated overhead canopy cover along 3, 36-m line transects centered on 1 side of the plot center tree. The first transect followed a randomly chosen bearing, with the second and third transects offset by 60° and 120° , respectively, to ensure that they sampled different portions of the plot. Sample points were located at 2-m intervals along the transects, except that we skipped points at 16 m, 18 m, and 20 m on the second and third transects to avoid oversampling at plot center (resulting n = 48 sample points).

At each point, we recorded the presence or absence of overhead canopy cover ($\geq 2 \text{ m high}$) using a sighting tube (Ganey and Block 1994).

At plot center, we recorded forest cover type (mixedconifer or other) and topographic position (drainage bottom or lower two-thirds of slope vs. upper third of slope or ridgetop). We estimated aspect (degrees) along the major slope axis, percent slope (sampled with a clinometer, taking 1 sample upslope and 1 downslope), and elevation (m, estimated using Garmin GPSMAP 60CSX units; Garmin International, Inc., Olathe, KS).

Data Analysis

We evaluated characteristics of nest trees and nest sites using spatially matched sets of plots, with each set consisting of a nest site plot and associated nest vicinity and PAC plots. We used 1 set of plots per owl territory in analyses, with all sets used anchored by a nest site used between 2002 and 2011. Our habitat data included 3 distinct data types: continuous covariates, categorical factors, and aspect, which was defined by a circular distribution. Because of the distinctly different data structures represented, we used different analytical approaches for each data type.

We used matched-case logistic regression (Hosmer and Lemeshow 2000) to compare continuous covariates of owl nest trees to center trees from random plots, and to compare nest site plots to random plots. This analysis modeled the difference between matched pairs of trees or sites, respectively. Because of the spatial matching described above, this means that each owl nest site was compared to random sites selected from its own neighborhood. Separate models were required to compare nest sites or trees to random sites or trees at the nest vicinity and PAC scales, respectively.

We developed 8 candidate models for comparisons of nest versus random trees; these included all possible combinations of the covariates modeled (tree dbh, tree height, and BVR). We predicted that nest trees would be larger in diameter, taller, and have a greater BVR than random trees.

In comparing characteristics of nest site and random plots, we formulated models using variables representing topography and various aspects of forest structure including canopy cover, tree and snag density and basal area, the large tree component, species composition, and decadence. We did not run all possible models at the site scale. Rather, we used subsets of these variables to develop a suite of 20 candidate habitat models. These models included variables that covered all aspects of forest structure, were suspected to influence habitat selection based on previous studies of Mexican spotted owls, and/or were amenable to manipulation by managers.

For both analyses (nest trees and nest sites), we ran matched-case logistic regression models using PASW Statistics 17.0 (SPSS, Chicago, IL), ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989), and report the set of competing models with Δ AIC_c ≤ 2 and their associated Akaike model weights (w_i ; Burnham and Anderson 2002).

We evaluated profile likelihood confidence intervals around parameter estimates in our top models, and considered confidence intervals that did not overlap zero to provide strong evidence for a significant model effect. We report mean differences between nest and random trees, and between nest site plots and random plots, as well as confidence intervals around those differences. As above, we considered confidence intervals that did not overlap zero to provide strong evidence for a significant difference. Because descriptors of nest tree and site characteristics may be more useful to managers than mean differences between trees and plot types, we also summarized descriptive characteristics of nest trees and sites (Appendices 1 and 2).

Because matched-case logistic regression models the difference between matched pairs, it does not handle categorical variables well. Consequently, we used chi-square tests (Zar 2009) to compare categorical variables between owl nest trees and random trees and between nest sites and random sites. We analyzed slope aspect separately, because it was represented by a circular distribution that was not amenable to analysis using matched-case logistic regression. We used Rayleigh's Z test to determine whether or not aspect values were significantly concentrated within plot type, and the Watson-Williams test to compare mean angles among plot types (Zar 2009). We conducted analyses using program Oriana, version 4 (Kovach Computing Services, Wales, United Kingdom). Neither of these latter approaches takes advantage of the spatial matching among nest and random plots.

We recognize that our analytical approach involves both information-theoretic and hypothesis testing paradigms. Although some authors argue that these paradigms should not be mixed (e.g., Anderson and Burnham 2002), we think that the combined approach we used presented the most reasonable approach, given the different data structures represented, and given that the different paradigms focused on different sets of variables (see also Stephens et al. 2005).

RESULTS

We analyzed nest tree and site characteristics using 63 sets of matched plots. Forest type did not differ significantly (P=0.303) among plot types, with most plots sampled occurring in mixed-conifer forest (92.1%, 87.3%, and 82.5% of nest site, nest vicinity, and PAC plots, respectively). This suggests that we were successful in restricting our random sites largely to the forest type most used by owls.

Characteristics of Nest Trees and Structures

All nests located were in trees (80.4% of nests) or snags. Species composition differed significantly (P < 0.001) between nest and random trees. Most nests were in white fir (42.9%) or Douglas-fir (49.2%), whereas white fir and Douglas-fir combined comprised only 63.5% of center trees in both nest vicinity and PAC plots. Top type also differed significantly (P < 0.001) between nest and random trees. Only 46% of nest trees had an intact top, versus 88.9% and 82.5% for random trees in nest vicinity and PAC plots,

respectively. Most nests were located in the upper half of tall, large diameter trees (Appendix 1).

Nests were located in cavities in trees or snags (48.2%), in large dwarf mistletoe witches brooms (36.1%), and in other platform types (12%; exact nest structure type was unknown for 3.8% of nest trees). Among cavity nests, 80.8% were in broken-topped trees or snags and 19.2% were in cavities formed in the side of trees or snags. Many nests (64.3%) in broken-topped trees were in trees where a secondary top had formed that provided shade and cover for the nest cavity. Most nests in dwarf mistletoe witches' brooms occurred in type II (43.6%) or III (28.2%) brooms, or in brooms that were either type II or type III, but where we could not determine the exact type (20.5%).

We evaluated 8 models comparing nest trees to center trees in random plots. Two competing models (i.e., $\Delta AIC_c < 2$) distinguished nest trees from nest vicinity center trees (Table 1). These 2 models collectively carried 99.9% of overall model weight, and model weights did not differ greatly between them. The top model included BVR, dbh (cm), and height (tree height in m), and the competing model included only BVR and dbh. Confidence intervals around parameter estimates did not include zero for any variables included in the top model (Table 2), suggesting that all had a significant effect. Nest trees had greater BVR and were larger in diameter and taller than nest vicinity center trees (Table 3). Confidence intervals around mean differences between nest and random trees did not include zero for any variables.

We also concluded 2 competing models distinguished nest trees from center trees on PAC plots. These models collectively carried 99.5% of overall model weight (Table 1). The top model included BVR and dbh, and the competing model included BVR, dbh, and height. The top model here was more than twice as likely as the next model. Confidence intervals around parameter estimates did not include zero for either variable in the top model (Table 2). Nest trees had

Table 1. Model results for competitive ($\Delta AIC_c < 2$) candidate models in matched-case logistic regression analyses comparing characteristics of Mexican spotted owl nest trees used from 2002 to 2011 and center trees sampled on other plot types in the Sacramento Mountains, New Mexico (n = 63 paired plots in each analysis).

Comparison and model ^a	AIC ^b	ΔAIC_{c}	w_i^{c}
Nest trees versus nest vicinity	trees		
BVR + dbh + height	22.796	0.000	0.550
BVR+dbh	23.202	0.406	0.449
Nest trees versus PAC trees			
BVR + dbh	46.301	0.000	0.688
BVR + dbh + height	47.915	1.614	0.307
BVR + dbh + height	47.915	1.614	0.307

^a Nest vicinity tree: >25-cm tree nearest randomly generated point within 200 m of the matched nest tree. PAC tree: >25-cm tree nearest randomly generated point within Protected Activity Centers (200–800 m from nest). Variables: BVR, broom volume rating, an index of dwarf mistletoe infestation ranging from 0 to 6, after Tinnin (1998); dbh, tree diameter at breast height (cm); height, tree height (m).

- ^b AIC_c = Akaike's Information Criterion corrected for small sample size (Hurvich and Tsai 1989).
- ^c Akaike model weights (Burnham and Anderson 2002).

Table 2. Parameter estimates (with SE and 95% CI) resulting from the top-ranked model in matched-case logistic regression comparisons of Mexican spotted owl nest trees used from 2002 to 2011 and center trees sampled in other plot types in the Sacramento Mountains, New Mexico (n = 63 paired plots in each analysis).

Comparison and variable ^a	Estimate	SE	95% CI
Nest trees versus nest vicinity	v trees		
BVR	1.504	0.313	0.891 to 2.118
Dbh	0.171	0.034	0.104 to 0.238
Height	-0.126	0.048	-0.220 to -0.032
Nest trees versus PAC trees			
BVR	0.688	0.209	0.278 to 1.098
Dbh	0.067	0.015	0.038 to 0.096

^a Nest vicinity tree: >25-cm tree nearest randomly generated point within 200 m of the matched nest tree. PAC tree: >25-cm tree nearest randomly generated point within Protected Activity Centers (200–800 m from nest). Variables: BVR, broom volume rating, an index of dwarf mistletoe infestation ranging from 0 to 6, after Tinnin (1998); dbh, diameter at breast height (cm); height, tree height (m).

greater BVR and were larger in diameter and taller than center trees on PAC plots, on average (Table 3). Confidence intervals around mean differences between nest and random trees did not include zero for BVR or dbh. In contrast, the confidence interval for height did overlap zero.

Characteristics of Nest Sites

Topographic position differed significantly among plot types (P=0.011). Eighty-one percent of nest site plots occurred in drainage bottoms or on lower slopes, with 19% on upper slopes and ridgetops. Many nest vicinity plots also occurred in drainage bottoms or on lower slopes (69.8%), whereas only 55.6% of PAC plots occurred in drainage bottoms or on lower slopes.

Nest site plots were significantly concentrated on northeasterly aspects (mean angle = 44.4°, 95% CI = 23.9-64.9°, P < 0.001, Rayleigh's Z test). Aspect also was significantly concentrated around the mean angle at nest vicinity plots (mean angle = 47.6°, 95% CI = 14.6-80.6°, P = 0.004). Mean angles did not differ significantly between nest site

Table 3. Differences (mean and 95% CI) between characteristics of Mexican spotted owl nest trees used from 2002 to 2011 and center trees from random plots in the Sacramento Mountains, New Mexico. Variables shown appeared in the top models distinguishing between nest and random trees. Estimates were based on 63 sets of matched plots.

	Difference ^a between nest tree and center trees from other plots			
	Nes	t vicinity	PAC	
Variable	Mean	95% CI	Mean	95% CI
BVR ^b Tree dbh (cm) Tree height (m)	0.933 28.2 2.8	0.463–1.404 21.5–34.9 0.5–5.2	0.750 21.6 2.5	0.257 to 1.243 14.4 to 28.9 -0.4 to 5.5

^a Computed as nest tree value—random tree value. Nest vicinity tree: >25cm tree nearest randomly generated point within 200 m of the matched nest tree. PAC tree: >25-cm tree nearest randomly generated point within Protected Activity Centers (200–800 m from nest).

^b BVR, broom volume rating, an index of dwarf mistletoe infestation ranging from 0 to 6, after Tinnin (1998).

Table 4. Model results for competitive ($\Delta AIC_c < 2$) candidate models in matched-case logistic regression analyses comparing forest structural characteristics of Mexican spotted owl nest sites used from 2002 to 2011 and random plots in the Sacramento Mountains, New Mexico (n = 63 paired plots in each analysis).

Comparison and model ^a	AIC	ΔAIC_{c}	w_i^{c}
Nest site versus nest vicinity			
Canopy cover $+$ % large tree basal area $+$ basal area of very large trees	54.071	0.000	0.332
Canopy cover $+$ basal area of very large trees $+$ large logs $+$ snag density	55.489	1.418	0.163
Canopy cover $+$ % white fir basal area $+$ % large tree basal area	55.963	1.892	0.129
Canopy cover + basal area of very large trees + large logs	55.997	1.926	0.127
Nest site versus PAC			
% white fir basal area $+$ canopy cover $+$ large tree density	45.312	0.0000	0.291
% White fir basal area + canopy cover + % large tree basal area	46.813	1.501	0.137
% white fir basal area + canopy cover + % large tree basal area + snag density	47.032	1.720	0.123

^a Nest vicinity: centered on random point within 200 m of the matched nest tree. PAC: centered on random point within Protected Activity Centers (200–800 m from nest). Variables: canopy cover = percent canopy cover, % large tree basal area = percent of total tree basal area in trees \geq 46 cm dbh (Seamans and Gutiérrez 1995, May et al. 2004), basal area of very large trees = basal area (m²/ha) of trees \geq 61 cm dbh, large logs = density (number/ha) of logs \geq 30 cm in mean diameter and 2.4 m in length, % white fir basal area = percent of total tree basal area in white fir, large tree density = density of live trees \geq 46 cm dbh. ^b AIC_c Akaike's Information Criterion corrected for small sample size (Hurvich and Tsai 1989).

^c Akaike model weights (Burnham and Anderson 2002).

and nest vicinity plots (P=0.840, Watson–Williams test). Aspect was not significantly concentrated around a mean angle at PAC plots (P=0.314). Variability around the mean angle increased from nest site to nest vicinity to PAC plots (CI widths = 41°, 66°, and 340°, respectively).

Four competing models distinguished nest site from nest vicinity plots (Table 4). These 4 models carried >75% of collective model weight. The top model included canopy cover, the percentage of total live tree basal area contributed by trees \geq 46 cm dbh (percentage of large tree basal area), and basal area (m²/ha) contributed by trees ≥ 61 cm dbh (basal area of very large trees), and was more than twice as likely as the next model. Canopy cover was included in all 4 competing models, and basal area of very large trees was included in 3 of the top models. Percentage of large tree basal area and density (number/ha) of large logs (defined after United States Department of Agriculture Forest Service 1996) each appeared in 2 models, and density of snags and the percentage of total live tree basal area contributed by white fir (percentage white fir basal area) each appeared in 1 of the top models. Confidence intervals around the parameter estimates did not include zero for any variables in the top model (Table 5). Owl nest sites had greater canopy cover, greater percentage of basal area contributed by trees \geq 46 cm dbh, and greater basal area contributed by trees \geq 61 cm dbh than nest vicinity plots (Table 6). Competing models indicated that owl nest sites had greater densities of large logs and snags than did nest vicinity plots, as well as a greater proportion of basal area contributed by white fir (Tables 4 and 6). Confidence intervals around mean differences between plots did not include zero for any variables except snag density (Table 6). Although the mean difference in snag density between nest site and nest vicinity plots was positive and relatively large, the associated confidence interval was extremely wide.

Analysis comparing nest site and PAC plots resulted in 3 competing models (Table 4). These models carried >55% of collective model weight. The top model included percentage white fir basal area, canopy cover, and density of trees

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 \geq 46 cm dbh (large tree density), and was more than twice as likely as the next model. Percentage white fir basal area and canopy cover occurred jointly in all 3 models, whereas large tree density appeared only in the top model. Percentage of large tree basal area appeared in 2 of the competing models, and snag density appeared in 1 competing model. Confidence intervals around the parameter estimates did not include zero for any variables in the top model (Table 5). Relative to PAC plots, nest sites had greater percentage of basal area contributed by white fir, greater canopy cover, and greater density of trees \geq 46 cm dbh (Table 6). Competing models indicated that owl nest sites also had greater proportion of basal area contributed by trees \geq 46 cm dbh and greater snag densities than PAC plots (Tables 4 and 6). As before, confidence intervals around mean differences between plots overlapped zero only for snag density (Table 6). Mean difference in snag density between plots was positive and relatively large, but the confidence interval was very

Table 5. Parameter estimates (with SE and 95% CI) resulting from the top-ranked model in matched-case logistic regression comparisons of forest structural characteristics of Mexican spotted owl nest sites used from 2002 to 2011 and random plots in the Sacramento Mountains, New Mexico (n = 63 paired plots in each analysis).

Comparison and variable ^a	Estimate	SE	95% CI
Nest site versus nest vicinity			
Canopy cover	7.469	2.128	3.330-11.640
% Large tree basal area	4.484	1.897	0.766-8.202
Basal area of very large trees	0.127	0.054	0.021-0.233
Nest site versus PAC			
% White fir basal area	4.960	1.472	2.075-7.845
Canopy cover	4.659	1.777	1.176-8.141
Large tree density	0.026	0.010	0.006-0.046

^a Nest vicinity: centered on random point within 200 m of the matched nest tree. PAC: centered on random point within Protected Activity Centers (200–800 m from nest). Variables: canopy cover = percent canopy cover, % large tree basal area = percent of total tree basal area in trees \geq 46 cm dbh, basal area of very large trees = basal area (m²/ha) of live trees \geq 61 cm dbh, % white fir basal area = percent of total tree basal area in white fir, large tree density = density (number/ha) of live trees \geq 46 cm dbh.

Table 6. Differences in forest structural characteristics between Mexican spotted owl nest sites used from 2002 to 2011 and matched random plots in the Sacramento Mountains, New Mexico. Also shown are mean differences between paired nest vicinity and PAC plots. Variables shown all appeared in at least 1 of the top models distinguishing nest sites from random sites. Estimates were based on 63 sets of matched plots.

	Nest site-nest vicinity ^b		Nest site-PAC ^b		Nest vicinity-PAC ^b	
Variable ^a	Mean	95% CI	Mean	95% CI	Mean	95% CI
Canopy cover	5.9	0.6-11.2	13.7	7.4-20.0	8.8	2.5 to 15.0
% Large tree basal area	15.2	8.1-22.3	12.9	5.4-20.3	-0.9	-11.1 to 9.2
Basal area of very large trees	4.9	2.7-7.1	3.6	1.3-5.8	-1.5	-3.8 to 0.9
Large logs	13.4	2.1-24.6	16.7	5.1-28.4	3.7	-5.9 to 13.3
Snag density	13.7	-49.3 - 76.9	29.1	-23.0-81.1	18.0	-49.2 to 85.1
% White fir basal area	9.2	1.1-17.2	23.1	14.8-31.4	15.6	6.8 to 24.5
Large tree density	19.0	8.7-29.4	25.1	15.3-35.0	5.6	-4.8 to 16.0

^a Variables: canopy cover = percent canopy cover, % large tree basal area = percent of total tree basal area in trees \geq 46 cm dbh, basal area of very large trees = basal area (m²/ha) of trees \geq 61 cm dbh, large logs = density (number/ha) of logs \geq 30 cm in mean diameter and 2.4 m in length, % white fir basal area = percent of total tree basal area in white fir, large tree density = density of live trees \geq 46 cm dbh.

^o Differences computed as nest site plot value–nest vicinity plot value, nest site plot value–PAC plot value, and nest vicinity plot value–PAC plot value, respectively. Nest vicinity: centered on random point within 200 m of the matched nest tree. PAC: centered on random point within Protected Activity Centers (200–800 m from nest).

wide. Overall basal area at nest sites was relatively high and the percentage of basal area contributed by ponderosa pine was extremely low (Appendix 2).

We did not model differences between paired nest vicinity and PAC plots. We did estimate mean differences between these plots for comparative purposes, however, using the variables identified as influential in models distinguishing nest site from random plots. Only 2 variables (canopy cover and percentage white fir basal area) had confidence intervals around mean differences that did not overlap zero (Table 4). Nest vicinity plots had greater canopy cover and percentage of basal area contributed by white fir than did PAC plots.

DISCUSSION

Previous studies of nesting habitat of Mexican spotted owl sampled random plots selected both within nest areas (similar to our nest vicinity scale) and within large study areas. However, results of these studies focused on comparisons involving random plots selected within large study areas and that were not restricted to areas likely to be used by owls or even to forest types selected by owls. These studies demonstrated that owl nest sites differed from random plots selected in these large study areas. In contrast, we selected random plots from areas that were within activity centers of resident owls and in the primary forest type used by these owls, and demonstrated that nest sites were unique even with respect to habitat available within these activity centers and forest type.

Despite the differences in spatial scales examined, our results generally support previous studies indicating that nesting Mexican spotted owls select unique trees and nest structures within a forested landscape. Those trees and structures show both similarities and differences among study areas. For example, owls in all study areas nested selectively in large trees, which presumably provide more nest structures (large cavities and platforms) than smaller trees. The types of trees and structures used varied among areas, however. Mexican spotted owls in the Sacramento Mountains nested in white fir and in cavities and broken-topped trees or snags more frequently than owls in other study areas (Seamans and Gutiérrez 1995, May et al. 2004). Cavities, especially cavities located in broken-topped trees, provide more favorable thermal environments than platform nests, (Rockweit et al. 2012). Cavity nests also typically last longer than platform nests (Folliard 1993, Forsman and Giese 1997). Thus, the cavities used here likely provide more stable and higher-quality nest sites than platform nests used here and elsewhere (Rockweit et al. 2012).

Other studies of Mexican spotted owl nesting habitat did not characterize broom volume rating for nest trees or quantify the types of brooms used. In studies of northern spotted owls (Strix occidentalis caurina) in Oregon, however, most nests in dwarf mistletoe brooms were located in type II and III brooms (Marshall et al. 2003), similar to our observations in the Sacramento Mountains. Northern spotted owls nested in large brooms, with minimum size of 1.7 m³ or about 1.2 m on a side (Martin et al. 1992). In a study of dwarf mistletoe brooms in Douglas-fir trees in southern Oregon, this minimum size was attained by all type III brooms sampled, by >67% of type II brooms sampled, but by only 33% of type I brooms sampled (Mallams et al. 2005). Thus, use of witches' brooms may be driven by broom size as well as type (Hedwall and Mathiasen 2006, Hedwall et al. 2006). We did not measure broom size, but many of the brooms used in the Sacramento Mountains were large and likely similar to or larger than the minimum size used by northern spotted owls.

Our results also generally support previous studies indicating that Mexican spotted owl nest sites differ from random sites. For example, owl nest sites in all study areas tended to cluster on northerly aspects, were concentrated on the lower two-thirds of slopes, and canopy cover and basal area of large trees emerged as influential variables distinguishing nest sites from random sites.

We observed 2 differences in forest characteristics between nest sites in the Sacramento Mountains and other study areas, however. One difference was white fir was a better predictor of habitat selection in the Sacramento Mountains than in other study areas. White fir did not appear in top habitat models in other study areas (Seamans and Gutiérrez 1995, May et al. 2004), whereas percentage white fir basal area appeared in our suite of top models at both spatial scales, and was 1 of only 2 variables (along with canopy cover) that declined from nest site plots to nest vicinity to PAC plots (Table 6). White fir contributed more than 50% of basal area at our nest sites, on average, and more than 50% of that white fir basal area was contributed by trees ≥ 46 cm dbh, indicating that most nest sites in the Sacramento Mountains were located in areas with large white fir trees.

The second difference was that oak and other hardwoods were better predictors of habitat selection in other study areas than in the Sacramento Mountains. Most nests sampled by Seamans and Gutiérrez (1995:945) occurred in mixedconifer forest where Gambel oak was dominant or codominant in the understory. Similarly, basal area of "mature/old growth hardwoods" was 1 of the most influential variables in habitat models evaluated by May et al. (2004: Table 5), and many nests were located in Gambel oak in their study area. In contrast, hardwoods were not included in our top models and only 1 nest was located in an oak in the Sacramento Mountains.

These differences have 2 important implications with respect to forest management. Southwestern mixed-conifer forests occupy a complex gradient ranging from dry forests with a history of frequent fire to wetter forests with a history of infrequent fire (Smith et al. 2008). Forests at the drier end of this gradient historically were relatively open in structure and were dominated by species such as ponderosa pine and Douglas-fir that were relatively fire tolerant and shade intolerant (Smith et al. 2008). In contrast, nest sites in the Sacramento Mountains were dominated by white fir, a species that is both shade tolerant and relatively intolerant to fire. The presence of white fir as a climax species is 1 of the indicators of a cooler and wetter mixed-conifer forest (Smith et al. 2008: Tables 2 and 5). Our results thus suggest that many owl nest sites in the Sacramento Mountains fall toward the cooler and wetter end of the mixed-conifer spectrum. These wetter mixed-conifer forests are characterized by relatively infrequent, moderate to high intensity fire regimes with return intervals ranging from 22 to 150 years, and later seral stages are characterized by closed-canopy forests (Smith et al. 2008: Table 5). Thus, many nesting areas used by owls in the Sacramento Mountains appear to be within the natural range of variability for wet mixed-conifer forest, suggesting that these areas are not in urgent need of restoration.

A second implication involves the greater influence of the oak-hardwood component in studies in drier forest types relative to the Sacramento Mountains. Nests sampled in previous studies occurred primarily in Douglas-fir (Seamans and Gutiérrez 1995) or in Gambel oak and ponderosa pine (May et al. 2004). These species are characteristic of drier mixed-conifer forests, suggesting that many of the nest sites sampled occurred either in mixed-conifer forests that fell toward the dry end of the mixed-conifer gradient or in other dry forest types (e.g., pine–oak; May et al. 2004). We suggest that these drier forests, which historically were subject to frequent fire that maintained a more open structure, may not attain the type of forest structure sought by nesting spotted owls without a well-developed hardwood component (see also Ganey et al. 1992, Stacey and Hodgson 1999). This in turn suggests that managers should retain and develop this hardwood component where spotted owls occur in drier forest types.

Our results are specific to our study area within the Sacramento Mountains, and the generality of these results is unknown. Mexican spotted owls in other areas may or may not be selecting wet mixed-conifer forest for nesting habitat. Given the recent management emphasis in southwestern national forests on distinguishing between wet and dry mixed-conifer forests, the differences between these types in the need for restoration, and the very different management approaches proposed to achieve forest restoration and desired future conditions, the relative use of wet versus dry mixedconifer forest by Mexican spotted owls across their range should be evaluated. This evaluation is currently hampered by the lack of an accurate digital map showing the spatial distribution of wet and dry mixed-conifer forest.

MANAGEMENT IMPLICATIONS

One of the challenges facing land managers in the southwestern United States is integrating habitat management for Mexican spotted owls with efforts to restore forests to structural conditions that existed prior to the advent of effective fire suppression efforts. Restoration treatments may not be urgently needed in the wet mixed-conifer types used by nesting owls in our study area, however.

Treatments in this landscape could minimize impacts to owl nesting habitat by focusing on drier forest types on ridge tops and upper slopes and on south- and west-facing slopes. Such treatments generally would target the areas most in need of restoration, and could reduce landscape-scale fuel levels and continuity while largely avoiding the areas selected by nesting Mexican spotted owls. Care should be taken to locate treatments far enough from existing nests to minimize potential effects on microclimate in the nest area, however.

Many owl nests in the Sacramento Mountains occurred in cavities in broken-topped trees. Managers should retain legacy trees with deformities such as broken tops, as these trees may develop into nest trees providing high quality nest sites (Rockweit et al. 2012). Owls in the Sacramento Mountains (and elsewhere; Seamans and Gutiérrez 1995, May et al. 2004) also nested in dwarf mistletoe witches' brooms. Although these platforms may provide lower quality nest sites than do cavities, they nonetheless provide valuable nesting substrates for owls. Consequently, managers should retain large trees with large type II and III witches' brooms in areas managed as owl nesting habitat (Hedwall et al. 2006).

Finally, because we have little experience in managing or creating the types of forest structure used by nesting owls, considerable uncertainty exists with regard to the effects of treatments on owls and their nesting habitat (Ganey et al. 2011). Consequently, any treatments in or adjacent to owl nesting habitat should be viewed as experimental, and the effects of those treatments on both forest structure and subsequent use by owls should be monitored. These treatments also should aim to retain relatively high canopy cover and basal area of large trees, as well as some of the decadent elements typical of nest patches, such as large snags and logs.

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Appendix 1. Selected characteristics of Mexican spotted owl nest trees in the Sacramento Mountains, New Mexico. Estimates shown were based on 108 nest sites used from 1996 to 2011, rather than on the subset of 63 nest sites representing independent owl territories used in model-selection analyses. We used data from all nest trees, including multiple trees used in some owl territories, in the belief that the larger sample would provide more descriptive information for managers.

Variable	Mean	95% CI	Range
BVR ^a	1.05	0.66–1.44	0–6
Tree dbh (cm)	71.4	65.3-77.4	32–124
Tree height (m)	23.6	21.9–25.3	7–39
Nest height (m)	15.6	14.4–16.7	6–29
Nest height (%) ^b	67.7	63.2–72.2	23.0-100.0

^aBVR, broom volume rating, an index of dwarf mistletoe infestation ranging from 0 to 6, after Tinnin (1998).

^b Nest height (%) = (nest height/tree height) \times 100.

Appendix 2. Selected forest structural characteristics of Mexican spotted owl nest sites in the Sacramento Mountains, New Mexico. Variables shown either appeared in 1 of the top models distinguishing nest plots from random plots or were considered informative to managers (e.g., live tree basal area, % ponderosa pine basal area). Estimates were based on 108 nest site plots used from 1996 to 2011, rather than the subset of 63 plots used in model-selection analyses. We used data from all nest sites sampled in the belief that the larger sample would provide more information for managers.

Variable ^a	Mean	95% CI	Range
Canopy cover	66.6	63.6–69.4	27.1-95.8
% Large tree basal area	52.9	49.3-56.4	7.0-88.0
Basal area of very large trees	10.4	8.9-11.9	0.0-33.6
Large logs	28.8	21.8-35.8	0.0-159.2
Snag density	192.0	159.6-224.4	0.0-1,028.4
% White fir basal area	48.7	43.9–53.5	0.0-100.0
Large tree density	65.2	59.0-71.4	9.8-147.3
Live tree basal area	35.6	33.1-38.1	9.7–99.6
% Ponderosa pine basal area	0.2	0.0–0.3	0.0–3.0