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HABITAT SELECTION BY MEXICAN SPOTTED OWLS IN NORTHERN ARIZONA

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ABSTRACT.—We compared use of seven habitat types to availability of those types within the home ranges of eight radio-tagged Mexican Spotted Owls (*Strix occidentalis lucida*). When all habitat types were considered simultaneously, habitat use differed from habitat availability for each owl. Patterns of habitat use varied among individuals and with respect to activity. Owls generally foraged more than or as frequently as expected in virgin mixed-conifer and ponderosa pine (*Pinus ponderosa*) forests, and less than expected in managed forests. Owls roosted primarily in virgin mixed-conifer forests. We also compared habitat characteristics among foraging, roosting, and randomly available sites. Habitat characteristics differed significantly among plot types. Both roosting and foraging sites had more big logs, higher canopy closure, and greater densities and basal areas of both trees and snags than random sites. Roosting sites had greater canopy closure, more big logs, and greater densities of both trees and snags than foraging sites. Mature forests appear to be important to owls in this region, and different forest types may be used for different activities. *Received 4 November 1992, accepted 21 December 1992.*

THE MEXICAN SPOTTED OWL (*Strix occidentalis lucida*) occurs throughout forested highlands and rocky canyonlands in the southwestern United States and Mexico (McDonald et al. 1991). This owl is often associated with virgin forests in northern Arizona (Ganey and Balda 1989a), but little is known about its habitat requirements or how timber harvesting might affect owl habitat. Populations of the closely related Northern Spotted Owl (*S. o. caurina*), which appear to be closely tied to old-growth coniferous forests in the Pacific Northwest (Forsman et al. 1984, Carey et al. 1990, 1992, Solis and Gutiérrez 1990, Thomas et al. 1990, Blakesley et al. 1992), are declining as timber harvesting reduces the amount of such forest (Forsman et al. 1984, 1988). As a result, concern has arisen over the potential effects of timber harvesting on Mexican Spotted Owls and their habitat. Because of this concern, the owl was recently listed as Threatened (Turner 1993).

Information on specific patterns of habitat use by Mexican Spotted Owls is needed to evaluate the potential effects of timber harvesting on this owl. Here we describe patterns of habitat use within the home ranges of radio-tagged Mexican Spotted Owls (third-order selection; Johnson 1980) at two different spatial scales. Specifically, we compare owl use of habitat types to the availability of those habitat types within owl home ranges, and identify habitat features consistently occurring in areas used by Spotted Owls.

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METHODS

We monitored radio-tagged owls on three study areas in northern Arizona. The San Francisco Peaks (SFP) study area is located 3 km north of Flagstaff, the Walnut Canyon (WC) study area 4 km southeast of Flagstaff, and the White Mountains (WM) study area approximately 27 km southwest of Alpine in east-central Arizona. Elevations range from approximately 1,830 to 2,160 m at WC, 2,130 to 2,650 m at WM, and 2,190 to 2,930 m at SFP. All three areas have relatively cool summers with frequent rainfall, and cold winters with extended periods of snow cover. Vegetation on all three study areas is predominantly coniferous forest. Ponderosa pine (*Pinus ponderosa*) forest dominates at lower elevations and on south-facing slopes, with mixed conifer forest prevalent on north-facing slopes and at higher elevations. Mixed-conifer forest is dominated by Douglas-fir (*Pseudotsuga menziesii*) and/or white fir (*Abies concolor*).

Eight adult owls were captured and radiotagged: both members of two pairs at SFP; both members of one pair at WC; and two males from adjacent drainages at WM. Methods and equipment used to capture, radio, and track Spotted Owls, as well as tracking periods for individual owls, were described in Ganey and Balda (1989b). Each time an owl was radio-located, we recorded the date, time, and activity type. We defined two activity types, assuming all day locations (sunrise-sunset) represented roosting owls and all night locations (30-min postsunset through 30 min before sunrise) represented foraging owls (Forsman et al. 1984).

Use of habitat types.—We used owl locations to generate minimum-convex-polygon home ranges for individual owls (Ganey and Balda 1989b). We assumed that all habitats within this area were available for use by the owls (Carey et al. 1992).

We recognized and mapped seven broad habitat types within these home ranges based on differences in species composition, habitat structure, and logging history. Four of these habitat types (virgin mixed-conifer forest, virgin mixed-conifer forest on rocky slopes, virgin ponderosa pine forest, and virgin ponderosa pine-oak-juniper forest) were unlogged. The remaining habitat types were managed mixed-conifer forest, managed ponderosa pine forest, and nonforested (Table 1).

Habitat polygons were identified on aerial photos and mapped on topographic maps using a zoom transfer scope. Polygon boundaries were verified through field reconnaissance. Area of each habitat type was measured within each home range using a digitizer. These areas served as measures of relative availability of habitats.

All owl locations were classified to habitat type. Roost locations were based on visual observations of owls, and assignment to habitat type was unambiguous. Foraging locations were based on remote triangulation, and there may have been some misclassification of habitats used. However, all remote triangulations were based on three or more bearings, and were obtained when the owls were not moving. Most error polygons (Springer 1979) were less than 4 ha, and locations were not concentrated near stand edges. Thus, we believe that misclassification was a minor problem, and have no reason to suspect consistent biases for or against particular habitats.

We used the methods of Neu et al. (1974; see also Byers et al. 1984) to test the hypothesis that owls used habitat types in proportion to their availability, and to determine which habitat types were used more or less than expected when that hypothesis was rejected. Tests were conducted separately for each owl.

The lack of independence of sequential observations is problematic in studies of animal movements (Swihart and Slade 1985). Carey et al. (1989) found that a three- to five-day period between successive observations was required for statistical independence in a study of Northern Spotted Owls in Oregon. We obtained a maximum of one roosting location per day, and most intervals between successive locations were more than five days. Therefore, we considered these roosting locations statistically independent.

In contrast, we obtained an average of 3.2 ± SD of 0.62 locations per owl per night of tracking ($\bar{x}$ = 43.9 ± 14.5 nights tracked per owl). The minimum interval between consecutive locations was 30 min, with longer intervals common when birds were moving (Ganey and Balda 1989b). Because foraging owls could move rapidly ($\bar{x}$ > 354 m/h; Ganey 1988) and habitat patches were often relatively small ($\bar{x}$ = 42.6 ± 67.8 ha), we assumed that owls could move easily among habitat types between successive locations. Therefore, we assumed these locations were biologically independent (Lair 1987) and suitable for use in statistical tests of habitat selection.

We evaluated this assumption by examining the amount of variation in subsamples of location data collected at various time intervals. Subsamples were created by bootstrap sampling, with 1,000 different subsamples created for each time interval (intervals ranged from one to seven days between successive locations). We used a chi-square test of heterogeneity

TABLE 1. Habitat types recognized for analysis of habitat use by Mexican Spotted Owls in northern Arizona. Acronyms in parentheses.

Virgin mixed-conifer forest (VMC).—Unlogged forests containing uneven-aged stands of Douglas-fir and white fir, frequently with strong component of ponderosa pine. Limber pine (*P. flexilis*) or southwestern white pine (*P. strobiformis*) often present. Understories dominated by small conifers and/or Gambel oak. Canopy height 20–35 m; canopy closure generally >70%. Stand age generally >200 years.

Virgin mixed-conifer forest on rocky canyon slopes (VMC-rock).—Unlogged forests similar in species composition to above, but situated on steep canyon slopes with large rock outcrops and cliffs interspersed. Canopy height 15–30 m; canopy closure variable. Stand age generally >200 years.

Managed mixed-conifer forest (M-MC).—Mixed-conifer forests similar to above types in species composition, but subjected to partial overstory removal through selective cutting or shelterwood harvest. Canopy closure and basal area generally lower than in above unlogged types.

Virgin ponderosa pine forest (VPipo).—Unlogged forests dominated (>50% of overstory trees) by ponderosa pine. Gambel oak an important component in many stands. Canopy height 20–35 m; canopy closure generally <60%. Stand age generally >200 years.

Managed ponderosa pine forest (M-Pipo).—Ponderosa pine forest similar to above type in species composition, but subjected to partial overstory removal, with consequent reductions in canopy closure and basal area.

Virgin ponderosa pine-oak-juniper (VPipo-O-J).—Sparse to dense stands of unlogged ponderosa pine with a mixture of other species including Gambel oak, Rocky Mountain pinyon pine (*P. edulis*), Rocky Mountain juniper (*Juniperus scopulorum*), alligatorbark juniper (*J. deppeana*), and Douglas-fir.

Nonforested areas (Nonforest).—Nonforested habitats, including grassy meadows (some containing widely scattered trees) and brushy areas dominated by cliffrose (*Cowania mexicana*) and mountain mahogany (*Cercocarpus* sp.) on rocky slopes.

TABLE 2. Chi-square statistics for comparisons of habitat use between bootstrapped subsamples and all foraging locations (df = 5; nonforest habitat type eliminated due to low use).

Interval[a]	Chi-square statistics			Number of differences[c]
	Mean	Variance	Maximum[b]	
1	3.24	2.55	9.33	0
2	3.97	3.24	11.31	1
3	3.82	3.58	13.94	3
4	5.01	4.22	13.72	5
5	3.95	3.64	12.88	4
6	3.71	3.95	12.73	4
7	3.88	3.68	12.00	1

[a] Number of days between successive locations.
[b] $X^2 = 11.07$, 5 df, $P < 0.05$.
[c] Number of times observed habitat use differed significantly ($P < 0.05$) between subsample and all foraging locations ($n = 1{,}000$ bootstrap iterations for each interval).

(Conover 1980) to compare habitat use in each subsample to overall habitat use. This allowed us to examine the effect of time between locations on observed patterns of habitat use.

Habitat characteristics.—Where owls used habitat types nonrandomly, we examined specific habitat characteristics within the home range. We sampled habitat characteristics on 167 0.04-ha circular plots representing randomly available, foraging, and roosting areas. The number of plots was limited by time constraints rather than based on statistical considerations. Because of our small sample of plots, we restricted the number of variables measured. The WC study area was excluded from this analysis because it was impossible to measure circular plots on the rocky cliffs present in many of the areas used by the owls. Therefore, analysis of habitat characteristics included only six owls on two study areas. Plots were distributed evenly among the home ranges of these six owls.

Random plots were mapped on topographic maps using randomly generated Universal Transverse Mercator (Grubb and Eakle 1988) coordinates within owl home ranges. To avoid bias when locating plots in the field, plots were first located as accurately as possible using map, compass, and altimeter. A number from 1 to 4 was then picked from a hat to select a cardinal direction, and a second number from 1 to 20 was picked to select a number of paces. The center of the plot was located by walking the indicated number of paces in the indicated direction.

Foraging locations were not sufficiently accurate to justify locating plots around single foraging locations. Owls foraged extensively and repeatedly in some areas, however. We placed all foraging plots within these heavily-used areas, assuming that owls foraged throughout the area. We used the randomization procedure described above to locate foraging plots in the field.

Because roosting plots were based on visual observations of roosting owls, they presented no problems in location. Only roost sites used on more than five occasions were selected for measurement. Thus, both roosting and foraging plots represented areas used repeatedly by owls, and may not represent the full range of habitats used.

We recorded the following variables within the circular plot: (1) diameter at breast height (DBH) of all trees and snags ≥10 cm in diameter; (2) number of small logs (down logs ≥10 cm and <30.5 cm at midpoint diameter and ≥3 m in length); (3) number of big logs (down logs ≥30.5 cm at midpoint diameter and ≥3 m in length); and (4) percent canopy closure. DBH was measured to the nearest 0.25 cm with a DBH tape. Canopy closure was estimated with a spherical densiometer along a 23-m line transect centered at the plot center and oriented north-south. Six measurements were taken at equal intervals along the transect, then averaged. From field data, we computed: (a) live tree and snag density (trees/ha); and live tree and snag basal area (m^2/ha). Basal area was calculated using DBH measures from individual trees and snags. All plots were measured by J.L.G., eliminating interobserver variation (Block et al. 1987) as a source of error.

We used a multivariate analysis of variance (MANOVA; Norusis 1988a) to test the hypothesis that habitat characteristics did not differ among plot types. Seven variables were used in the MANOVA: number of small logs, number of big logs, canopy closure, live tree density, snag density, live tree basal area, and snag basal area. We used univariate analysis of variance (ANOVA) to examine patterns for individual habitat variables, and Scheffe's multiple-range test to identify which plot types differed significantly for individual variables. We chose the Scheffe test because it is conservative, requiring larger differences between population means for significance than most multiple-comparison methods (Norusis 1988b; B-156).

RESULTS

We observed few significant differences (18/7,000; Table 2) when we compared subsamples of foraging-location data to the entire set of foraging locations. In other words, patterns of habitat use observed in samples containing locations collected at intervals ranged from one to seven days between successive locations did not differ from the pattern of habitat use observed when all locations were included. We interpreted this as strong evidence for lack of autocorrelation among successive observations, and used all locations in analysis of habitat selection for foraging.

TABLE 3. Percent home-range composition and habitat use (composition/foraging use/roosting use) for eight Mexican Spotted Owls in northern Arizona, 1986–1987. Habitat types described in Table 1.

			Habitat type[b]						
Owl	Sex	n[a]	VMC	VMC-rock	VPipo	VPipo-O-J	M-MC	M-Pipo	Non-forest
WC	M	163/38	0/0/0	17/41^{+}/79	6/12/11	11/33^{+}/3	0/0/0	65/14^{-}/8	1/0/0
WC	F	190/39	0/0/0	17/44^{+}/85	6/7/5	13/32^{+}/5	0/0/0	62/16^{-}/5	2/1/0
SFP1	M	137/22	48/59/82	7/2^{-}/9	13/16/9	6/7/0	4/2^{-}/0	15/15/0	7/0^{-}/0
SFP1	F	132/20	45/42/65	8/9/5	13/15/25	7/18^{+}/5	5/2^{-}/0	14/14/0	8/0^{-}/0
SFP2	M	204/62	20/27/62	0/0/0	14/33^{+}/26	0/0/0	7/3^{-}/2	58/36^{-}/10	0/0/0
SFP2	F	201/40	28/30/87	4/13^{+}/8	12/34^{+}/5	0/0/0	4/4/0	50/17^{-}/0	2/2/0
WM1	M	155/22	25/62^{+}/100	0/0/0	9/24^{+}/0	0/0/0	13/7^{-}/0	53/8^{-}/0	0/0/0
WM2	M	153/18	34/59^{+}/78	0/0/0	15/24^{+}/17	0/0/0	35/13^{-}/6	15/3^{-}/0	1/1/0

[a] Number of locations for foraging/roosting.

[b] Positive or negative sign indicates that habitat used significantly more than (+) or less than (−) expected ($P < 0.05$). Roosting use not compared statistically due to small sample sizes.

Use of habitat types.—Radio-tagged owls foraged in all habitat types, and used more than one habitat type on 157 of 208 nights (75.5%) when three or more locations/owl were obtained. All individual owls used habitat types nonrandomly ($P < 0.01$). Owls generally foraged more than or as frequently as expected in virgin forests and less than expected in managed forests (Table 3). Some owls used managed forests as frequently as expected, but none used such forests more than expected. There was little use of nonforested habitats.

Patterns of habitat availability and use varied among individuals and study areas. Both owls at WC foraged primarily in virgin mixed-conifer forest on rocky slopes and virgin ponderosa pine-oak-juniper forest (Table 3). Both of these habitats contained rocky cliffs and outcrops interspersed with forested areas. Telemetry locations were not sufficiently accurate to determine whether the owls were foraging among trees or rocks, but observations at dusk and vocalizations suggested that owls used both habitat components extensively.

Patterns of habitat use were also relatively consistent at WM, where both owls used virgin mixed-conifer and ponderosa pine forests more than expected, and managed forests less than expected (Table 3). Habitat use was more variable at SFP. The SFP1 pair consistently used nonforested habitat and managed mixed-conifer forest less than expected, but used most other habitats (70% of possible comparisons; Table 3) in proportion to availability. Both members of the SFP2 pair used virgin ponderosa pine forest more than expected, and managed ponderosa pine forest less than expected (Table 3). There also were differences in habitat use patterns within pairs at SFP.

Small samples precluded statistical analysis of habitat selection for roosting by individual owls. Most owls roosted primarily in virgin mixed-conifer forests, with some also roosting in virgin ponderosa pine forest (Table 3). The remaining forest types received little or no use (≤10%) for roosting. Ponderosa pine stands used by roosting owls contained Douglas-fir and white fir and/or a dense understory of Gambel oak (*Quercus gambelii*). The WC owls often roosted in trees at the base of north-facing cliffs, on the cliffs themselves, or in caves.

Habitat characteristics.—Habitat characteristics differed significantly among plot types (MANOVA; $F_{2,164} = 13.3$, $P < 0.001$). All seven habitat variables differed significantly (ANOVA) among plot types (Table 4). Based on multiple-range tests, all variables differed significantly between roosting and random plots. Values were higher for all variables on roosting plots (Table 4). Roosting plots also had significantly more big logs, higher percent canopy closure, and greater densities of both live trees and snags than foraging plots. Foraging plots differed significantly from random plots for all variables except number of small logs; all values were higher on foraging than on random plots (Table 4).

DISCUSSION

All radio-tagged owls in this study used available habitat types nonrandomly. There was con-

TABLE 4. Habitat characteristics ($\bar{x} \pm$ SD) measured on 0.04-ha circular plots within home ranges of Mexican Spotted Owls in northern Arizona.

	Plot type			
Variable	Roosting (n = 33)	Foraging (n = 66)	Random (n = 67)	F[a]
Small logs/ha	148.2 ± 95.7	116.8 ± 97.0	96.3 ± 86.1	3.5*
Big logs/ha	122.8 ± 66.1	83.5 ± 57.9	47.9 ± 46.3	21.1***
Canopy closure (%)	79.1 ± 5.2	67.1 ± 10.9	51.7 ± 18.8	46.3***
Trees/ha	812.9 ± 334.3	646.7 ± 288.0	445.3 ± 277.0	19.0***
Snags/ha	97.3 ± 66.8	55.1 ± 48.2	22.5 ± 30.1	29.4***
Tree basal area (m^2/ha)	52.3 ± 16.4	47.5 ± 13.5	29.9 ± 14.0	37.6***
Snag basal area (m^2/ha)	8.9 ± 8.2	6.4 ± 7.1	2.4 ± 3.7	13.9***

[a] ANOVA, df = 2 and 164. *, $P < 0.05$; ***, $P < 0.001$.

siderable variation among individuals in use of foraging habitat, however. Whether this variation is due to individual variation in the owls themselves or to differences in habitats among areas is not clear.

Despite differences among individuals, there were consistent trends in use of foraging habitat. In general, owls foraged more than or as frequently as expected in virgin forests, and less than expected in managed forests. They showed very low use of nonforested habitats. Perhaps the most striking pattern with respect to foraging habitat was the consistent avoidance of managed forests (11 of 14 possible comparisons; Table 3). This avoidance was demonstrated more clearly than was a corresponding preference for virgin forests. Mexican Spotted Owls may differ in this respect from Northern Spotted Owls, which show a strong preference for mature and old-growth forest when foraging (Forsman et al. 1984, Carey et al. 1990, 1992, Solis and Gutiérrez 1990). We wish to stress, however, that we refer here only to third-order selection (as defined by Johnson 1980) by foraging owls. Selection for virgin forests may well occur at higher orders (see Blakesley et al. 1992) or for other activities (see below). The managed stands on our study areas typically were uneven-aged stands resulting from partial overstory harvests. In contrast, most managed stands within areas where radio-tagged Northern Spotted Owls have been studied were even-aged stands resulting from clearcut logging. These stands thus differ greatly in structure, and perhaps also in their suitability for use by Spotted Owls.

There also may be differences between Mexican and Northern Spotted Owls in foraging behavior. Carey et al. (1992:228; see also Carey et al. 1989:12) reported that Northern Spotted Owls generally remained in the same stand while foraging. This was clearly not the case with respect to the owls in this study, which generally used more than one habitat type per night. This difference is even more striking because habitat patches were apparently larger on average in our study ($\bar{x}$ = 42.6 ± 67.8 ha) than in Carey et al.'s (1989:12) study, where "one-half to two-thirds of the patches were 20 ha or less."

Habitat-use patterns also differed with respect to activity type. Some owls foraged preferentially in either virgin mixed-conifer or ponderosa pine forests (or both), but all roosted primarily in virgin mixed-conifer forests (Table 3). This suggests that Mexican Spotted Owls use virgin ponderosa pine forests mainly for foraging, and that they use a wider variety of habitats for foraging than for roosting. In studies of California Spotted Owls (*S. o. occidentalis*), Laymon (1988) and Zabel et al. (1992:153) also observed greater variability in foraging than in roosting habitat. In contrast, Solis and Gutiérrez (1990) and Carey et al. (1992) found no differences between habitats used for roosting and foraging by Northern Spotted Owls.

Mexican Spotted Owls are associated with virgin mixed-conifer forests throughout much of northern Arizona (Ganey and Balda 1989a). Although virgin mixed-conifer forests were used for both foraging and roosting in our study, roosting owls showed the strongest affinity for these forests. Thus, the association between the owls and virgin mixed-conifer forests may be driven mainly by the availability of suitable roosting (and nesting) habitat, and such habitat may be more limiting than suitable foraging habitat in this area.

Results of analyses of habitat characteristics are consistent with the observed patterns of use of habitat types. Both foraging and roosting plots were readily distinguished from random plots using variables related to forest structure. Foraging and roosting plots were more similar to each other than to random plots (Table 4), but there were differences between areas used by owls for roosting and foraging. Owls roosted primarily in decadent, closed-canopy stands with high densities of trees and snags and many big logs, whereas foraging was not confined to such areas (Table 4). This again suggests a greater selectivity for roosting habitat.

The habitat characteristics differing among plot types (Table 4) represent structural features common in but not restricted to virgin forests. This may explain why some managed stands were used by foraging owls. These areas may have contained some or all of the habitat features preferred by Spotted Owls. Identification of such features is an important step toward understanding actual habitat requirements of Spotted Owls in northern Arizona.

Knowing why owls select particular habitat features also is important in order to understand their habitat requirements. Unfortunately, we can only speculate at present. The consistent selection of dense, closed-canopy forests for roosting may indicate that owls were seeking favorable microclimatic conditions, as suggested by Barrows (1981; see also Ganey et al. 1993). The frequent use of caves and north-facing cliffs by the WC owls is consistent with this interpretation. The high snag densities observed in most roost areas may be a result of the overall decadence of these areas, and not directly tied to owl roosting behavior. Although we have observed owls foraging from and especially calling from snags, we have rarely observed them to roost in snags.

The high basal areas and numbers of down logs observed in high-use foraging areas may relate both to foraging behavior and prey availability. Forests with high basal areas likely provide abundant foraging perches for owls. The numerous logs present in many foraging areas may be important in providing homes and hiding cover for the small mammals on which the owls prey (Ganey 1992). Snags also may provide homes for small mammals on occasion.

There are several problems in interpretation of our analyses of habitat characteristics. Because of the way in which plots were selected, both foraging and roosting plots represent areas used repeatedly by owls. These areas may not represent the full range of habitats used by owls for roosting and, especially, for foraging. Also, because of small sample sizes, we pooled plots across individuals for our analyses. In light of the differences among individuals in use of habitat types, this pooling may not be fully justifiable. Finally, we assumed that areas used repeatedly by owls at night represented foraging areas. In fact, we cannot be certain that they were not resting in these areas.

Despite these problems, the variables identified as important in these exploratory analyses are consistent with descriptions of Spotted Owl habitat in other areas (Forsman et al. 1984, Laymon 1988, Carey et al. 1990, 1992, Solis and Gutiérrez 1990). We consider the emerging patterns to be a first step towards understanding the habitat requirements of Mexican Spotted Owls in Arizona mixed-conifer and ponderosa pine forests. We caution that habitat characteristics may be very different in other areas or habitats, however. For example, rocky cliffs appeared to provide suitable habitat for both foraging and roosting owls at WC.

Because our study was based on only eight owls, the generality of the results is open to question. For example, some Mexican Spotted Owls are known to occupy areas lacking virgin forests (Kertell 1977, Wagner et al. 1982, Ganey and Balda 1989a), which were preferred for both foraging and roosting by the owls in our study. Future studies should examine Spotted Owl habitat in more detail, should address the nature and extent of individual variation in habitat use, and should attempt to identify important habitat characteristics of managed stands used by owls. Until better information is available, however, management of Spotted Owl habitat should be approached conservatively. The consistent avoidance of logged stands and the use of mature or virgin stands at levels greater than expected argue for retention of virgin (or at least mature) forests in areas occupied by Mexican Spotted Owls. The use of different forest types for different activities suggests that virgin stands of both mixed-conifer and ponderosa pine forest should be retained, so as to provide suitable habitat for both foraging and roosting.

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