Biological Diversity in Montane Riparian Ecosystems: the Case of the Mexican Spotted Owl

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Abstract—Although usually considered to be a bird of old growth mixed conifer forests, the Mexican spotted owl historically occurred in a wide range of habitats from lowland cottonwood bosques to montane canyon systems. In a recent study of habitat use in central New Mexico, we found that owls roost primarily in canyon bottoms, and that they select sites that are characterized by deciduous trees and high structural complexity of vegetation, rather than by large diameter conifer trees per se. Intact riparian areas in montane canyons typically have considerable structure, yet, as in the lowlands, these habitats have undergone extensive modification and reduction. The unexpected diversity of habitat use of the Mexican spotted owl suggests that historic changes in upland riparian systems in the Rio Grande Basin may have impacted more species than originally believed.

Although the Mexican spotted owl (*Strix occidentalis lucida*) is often considered to be a species that depends primarily upon mature mixed-conifer forest, it actually is known to have historically nested in a surprisingly large range of habitats. For example, spotted owls once occurred in the lowland cottonwood bosques of New Mexico and Arizona (Bailey 1928, Phillips and others 1964), and even today they can still be found in some Arizona cypress and Maderan oak forests in SE Arizona (USDI Fish and Wildlife Service 1995). At the present time, however, most spotted owls in the Rio Grande Basin and throughout the southwest are restricted to canyon habitats at higher elevations in the mountains. The topography of these mountain systems can be extremely complex, and exposure, soil types and moisture regimes often vary over extremely short spatial scales. As a result, the vegetation communities within a particular owl territory may actually consist of a complex mosaic of plant associations that range from mixed conifer forests (usually dominated by Douglas-fir, *Pseudotsuga menziesii*, and southwestern white pine, *Pinus strobiformis*) on north facing slopes, ponderosa pine (*P. ponderosa*) forests on east and west facing slopes, and pinyon-juniper (*P. edulis* and *Juniperus* spp.) forests or scrub oak (*Quercus*) thickets on south facing slopes. In the canyon bottoms themselves, vegetation may range in some locations from relative intact riparian forests dominated by narrow-leaf cottonwood (*Populus angustifolia*) and oak (primarily Gambel oak, *Quercus gambelii* and gray oak, *Q. grisea*), to open pine-oak meadows in areas that have been heavily impacted by livestock grazing (for a detailed description of these associations, see Dick Peddie 1993). Because of the floristic complexity that exists within most spotted owl territories in the southwest, it has not always clear which plant associations within the mosaic are actually important to the birds, and therefore which types of habitat modification may be most likely to adversely affect their continued survival.

Because the spotted owl has played a central role in controversies over timber harvests on public lands in the southwest and elsewhere, most previous studies of habitat selection in this subspecies have focused upon their association with large and/or commercially important conifer trees (Ganey and Balda 1994, Zwank and others 1994, Seamans and Gutierrez 1995). These studies found that spotted owls tend to roost or nest in areas that have more or larger diameter conifer trees than when compared to randomly chosen sites, and that they tend to use unmanaged conifer forests more often than would be expected by chance alone. However, these studies did not specifically examine the importance of other species such as the deciduous oaks and cottonwoods that often occur in the understory of canyon bottoms, although most authors have noted that oaks are common at many roost sites (see also Ganey and others 1992). Rinkevich and Gutierrez (1997) found that in Zion National Park in Utah, Mexican spotted owls are found only in canyon bottom habitats with well-developed riparian vegetation, and that they are absent from the pure mixed conifer forests on the plateaus at the tops of the cliffs. Similarly, there are no established nesting territories of spotted owls in the extensive mixed conifer forests on the Kiabab Plateau in northern Arizona, even though there are a number of birds in the canyons that radiate from the plateau (J. Goodman, pers. comm.; R. Silver, pers. comm.). These observations, when combined with the historical records of owls nesting in lowland riparian forests in the complete absence of mixed-conifer, suggest that tree species or vegetative characteristics other than, or in addition to, large diameter conifer trees, may be important in habitat selection in this subspecies.

The goal of this project was to explore this question for spotted owls that occur in montane canyon habitats in the middle Rio Grande basin of west-central New Mexico. Although we used the same general methods to study habitat selection as most prior studies (Ganey and Balda 1994, Zwank and others 1994, Seamans and Gutierrez 1995), we expanded our analysis in several ways. First, we included

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both conifer and deciduous trees when sampling vegetation composition and structure in the roosting and randomly selected plots. Second, we recorded the presence in our plots of smaller diameter trees (>5 cm D.B.H.) than were included in previous studies (usually >10 cm D.B.H.), since many deciduous trees, particularly oaks, have small stem diameters and would otherwise be excluded from our analysis. And finally, in recognition of the high degree of spatial heterogeneity in the vegetation of owl territories, we undertook two different statistical comparisons. First, as was done in previous studies, we compared occupied owl roost sites with randomly chosen sites that were located within all of the different plant community types within the owls' territories (for example, pinon-juniper, ponderosa pine, deciduous/riparian, etc.). However, since we found that the owls did not actually use all of these associations for roosting, we conducted a second analysis in which we restricted the comparison of roost sites to only the subset of random plots that were located within the same vegetation associations used by the owls (mixed conifer/deciduous and mixed conifer; see below). The first comparison will reveal the general types of habitats or plant associations that the owl uses for roosting, while the second analysis examines the *specific characteristics of the vegetation* that appear to be important for habitat selection within that particular association(s). This second analysis is particularly useful in management, because it can give detailed information on the important habitat characteristics of the associations that are actually used by the owls, and therefore might be affected by different management activities within those associations.

Methods

Study Areas

The data reported here were collected as part of a long-term study of the Mexican spotted owl in west central New Mexico (Arsenault and others 1997, Kuntz and Stacey 1997). Our primary location for the roost-site analysis was located in the West Red canyon area of the San Mateo Mountains, 40 km west of the Rio Grande near Truth or Consequences, NM. Owls have been recorded in this canyon since at least the early 1900's (Ligon 1926) and we believe it represents habitats typical of those now occupied by this species in many of the mountain ranges in the southwest. The topography is characterized by deep forested canyons that extend from a central ridge of peaks that runs north-south along the length of the mountain chain. Elevations at the study site vary from 1800-3200 m, and the vegetation is a mix of scrub oak, pinyon-juniper, ponderosa pine, mixed conifer, and limited aspen and spruce-fir at the highest elevations (see Dick-Peddie 1993). Remnant riparian vegetation, consisting primarily of Gambel oak and scattered mature narrow-leaf cottonwood trees, occurs along all canyon bottoms. At the present time, there is little or no regeneration of the cottonwoods and most have died off. However, dense stands of cottonwood, willows (*Salix* spp.) and other riparian species can be found within livestock exclosures in West Red and elsewhere in the San Mateo Mountains, and we believe this to be the original vegetation association in the canyon bottoms. But because the current vegetation has been extensively altered from its original condition, we refer to this association as "mixed-conifer/deciduous", since it is now dominated by conifers and oak trees, with mature cottonwoods in some locations. Most of the pure ponderosa pine and mixed-conifer forests in the San Mateos have been logged at least once during the past 50-100 years, although there is no timber harvest at present. The current land uses are primary livestock grazing (both summer and fall seasons) and recreation.

Detailed observations were made within three adjacent owl territories in the West Red Canyon watershed with a combined area of approximately 36 km^2. Additional qualitative assessments of owl roost areas were made in three other mountain ranges in west-central New Mexico, including the Black Range, the Magdalena Mountains and the Zuni Mountains. Vegetation in these ranges was similar to that of the San Mateo Mountains.

Habitat Analysis

We examined roosting habitat use from May through November, 1993-94. Spotted owls were first located during night surveys using standard techniques (Foresman 1983) and roost locations then determined the following day. We captured adult and juveniles at the roost using either a Bal-chatri trap or a 3.4 m noose pole. Each bird was then banded with an US Fish and Wildlife Service aluminum leg band and one color band. A 5 or 7.5-gram radio transmitter (Holohil Systems, Ltd., Woodlawn, Ontario, Canada) was then mounted on a central tail feather. The radio-tagged owls were then located 2-3 times per week while roosting, using a TRX 1000S radio telemetry receiver and a three-element Yagi antenna (Wildlife Materials, Inc., Carbondale, IL). The telemetry data were used to map the owls' breeding season home ranges using the minimum convex polygon method and the computer program CalHome (California Department of Fish and Game, Sacramento, CA). We marked the location of all roost locations, and all habitat measurements were taken at a later time when owls were not present. Roost sites within 50 meters of each other were considered part of the same cluster, even if they were used in different years. We did not include in the analysis any roost sites that were within 50 m of active nests, since spotted owls do not make their own nests, and instead must use either natural platforms in trees or caves, or the abandoned stick nests of other species. Since this could limit habitat choice, we examined roost locations of only non-breeding owls, or of family groups that had moved at least 100 meters from their nests.

We examined microhabitat characteristics within 0.04 ha circular plots at 64 breeding season (1 March-15 October) roost sites of radio-tagged owls and 69 random sites in the West Red Canyon study area. All random plots were located within the breeding season home ranges of the owls as determined by the radio-tracking. We used a random number table to generate UTM coordinates and then located the plot in the field using a Trimble global positioning system (Trimble Navigation, Sunnyvale, CA) with an accuracy of approximately 10-15 meters. Sample plots were centered on the roost tree or on the potential roost tree closest to the center of each random plot. The number of sites measured was limited by time constraints and was not determined by statistical methods.

We measured 27 variables within each plot. A complete description of each variable and additional details of sampling methods is given in Hodgson and Stacey (1996). We recorded the species identity, height, and diameter at breast height (D.B.H.) for each tree > 5 cm D.B.H. within each plot using a D.B.H. tape and clinometer. We then calculated the basal area (m^2/ha) and density (trees/ha) for each species, and height and diameter classes of trees. We used a compass to measure the aspect at the center of the plot and placed each plot in one of eight directional categories. Canopy closure was measured as the average of four densitometer readings taken 5 meters from the center of the plot in each of the four cardinal directions, as well as the position of the plot along the slope (upper 1/3, middle 1/3, lower 1/3 of slope, or drainage bottom) and height of the owl roost. Each plot was also assigned to one of four forest general types: mixed-conifer, ponderosa pine woodland, pinyon/juniper woodland, or mixed-conifer/ deciduous, as defined above. Juniper, pinyon pine and shrub live oak are the characteristic species of the pinyon/juniper woodland in this area, and we combined density and basal area of these species and designated the total as pinyon/juniper basal area and density.

Statistical Analysis

Means (± SD) were calculated reported for all habitat variables. Most variables were not normally distributed and could not be normalized using standard transformations. To determine if there was non-random selection for habitat characteristics associated with roost sites, we compared random and roost plot variables using the non-parametric Mann-Whitney U test (SAS 1988). Since there was a total of 45 individual variables that could be tested with the same data set (Hodgson and Stacey 1996), the significance level for each test was conservatively set at $p \le 0.005$, using the Bonferroni correction for 50 tests (Manly 1992). We analyzed the categorical variables, direction, position and forest type using Chi-square goodness-of-fit tests (SAS 1988).

Two different analyses were performed. First, to examine habitat selection within the entire range of vegetation associations present within the owls' home ranges, we compared roost sites to all of the random plots. Second, to determine if there was also non-random selection of roost sites within used forest types, the statistical influence of random plots in unused forest types (see Results) was removed by eliminating all plots that were in ponderosa pine or pinyon/juniper habitats from the random plot data set, since owls were never actually observed roosting in these forest types. All statistical analyses were then repeated using the subset of random plots that were located within mixed-conifer or mixed-conifer/ deciduous oak (n = 36).

Results

Roost Locations

As part of our overall study, we located roosting sites between 1993 and 1995 in 30 different spotted owl territories in four mountain ranges in addition to the three primary territories in West Red Canyon area. Owls in these areas had strong fidelity to breeding season roost sites: owls in 10 territories were found in the same roost areas for each of the three consecutive years, and for two years in nine other territories. In only three territories were owls found in different roost areas in consecutive years. Not every territory was occupied every year, and four occupied territories were checked during only one year. Four territories were checked for three consecutive years but owls were only located in those territories during only one year.

Twenty-eight (85 percent) of 33 different roost areas were located in canyon bottoms. Five roost areas (15 percent) were not associated with drainage bottoms and owls roosted on the upper or middle third of the slope in or adjacent to large rock cliffs. All 28 roost areas located in canyon bottoms had conifers (predominately Douglas-fir, ponderosa pine, and/or southwestern white pine) and deciduous trees within 30 meters of the roost site. Gambel oak was always present, and four roost areas also contained remnant cottonwoods. Sixteen of the canyon bottom roost areas were located in main (2nd or 3rd order) canyons and 12 were located in narrow first order drainages off of the main canyon. Of the five roost areas located in or near cliffs, four had only conifer trees within 30 meters of the roost site, while one also had Gambel oak.

Habitat Selection

The roost sites of six adult and three juvenile radio-tagged owls from the three territories in the San Mateo Mountains were used for the detailed habitat analysis. Habitat use by these birds was clearly non-random. Over two-thirds of the roost sites were located in the mixed-conifer/ deciduous association (49 of 64) and the remaining sites were in mixed-conifer (15/64). No owls were found to roost in pinon-juniper or ponderosa pine forests. The distribution of roost plots among forest types was significantly different from the distribution of random plots within the owls' home ranges ($\chi^2 = 230.8$, df=3, $p < 0.001$, fig. 1). Percent canopy closure in roost plots ($\bar{x} = 59.2 \pm 17.2$) was significantly greater than in the full set of random plots representing all forest types ($\bar{x} = 42.6 \pm 20.1$, $p < 0.001$) but was not significantly different from mean canopy closure in the random plots in only the mixed-conifer and mixed-conifer/ deciduous associations ($\bar{x} = 51.9 \pm 18.7$, $p = 0.0751$). The density of live trees was significantly greater in roost sites ($\bar{x} = 773.1 \pm 328.4$) then in random sites in all forest types ($\bar{x} = 577.9 \pm 354.1$, $p < 0.001$) but did not differ from random sites in mixed-conifer and mixed conifer/deciduous associations ($\bar{x} = 703.5 \pm 380.3$, $p > 0.05$). Mean roost tree D.B.H. was 31.1 ± 14.3 cm, mean roost tree height was 18.4 ± 6.8 meters, and mean owl roost height was 5.3 ± 2.2 meters. Most Mexican spotted owls roosted in live Douglas-fir (47 percent), Gambel oak (19 percent), or Southwestern white pine trees (13 percent).

A comparison of the basal area of tree species found in roost plots to that in random plots in all forest types (the overall comparison; table 1) found significantly higher basal area of Douglas-fir, southwestern white pine, and Gambel oak/ other deciduous trees, and significantly lower pinon/ juniper, in the roost plots. In contrast, when the roost plots were compared only to the subset of random plots within used habitats, the differences in Douglas-fir and white pine

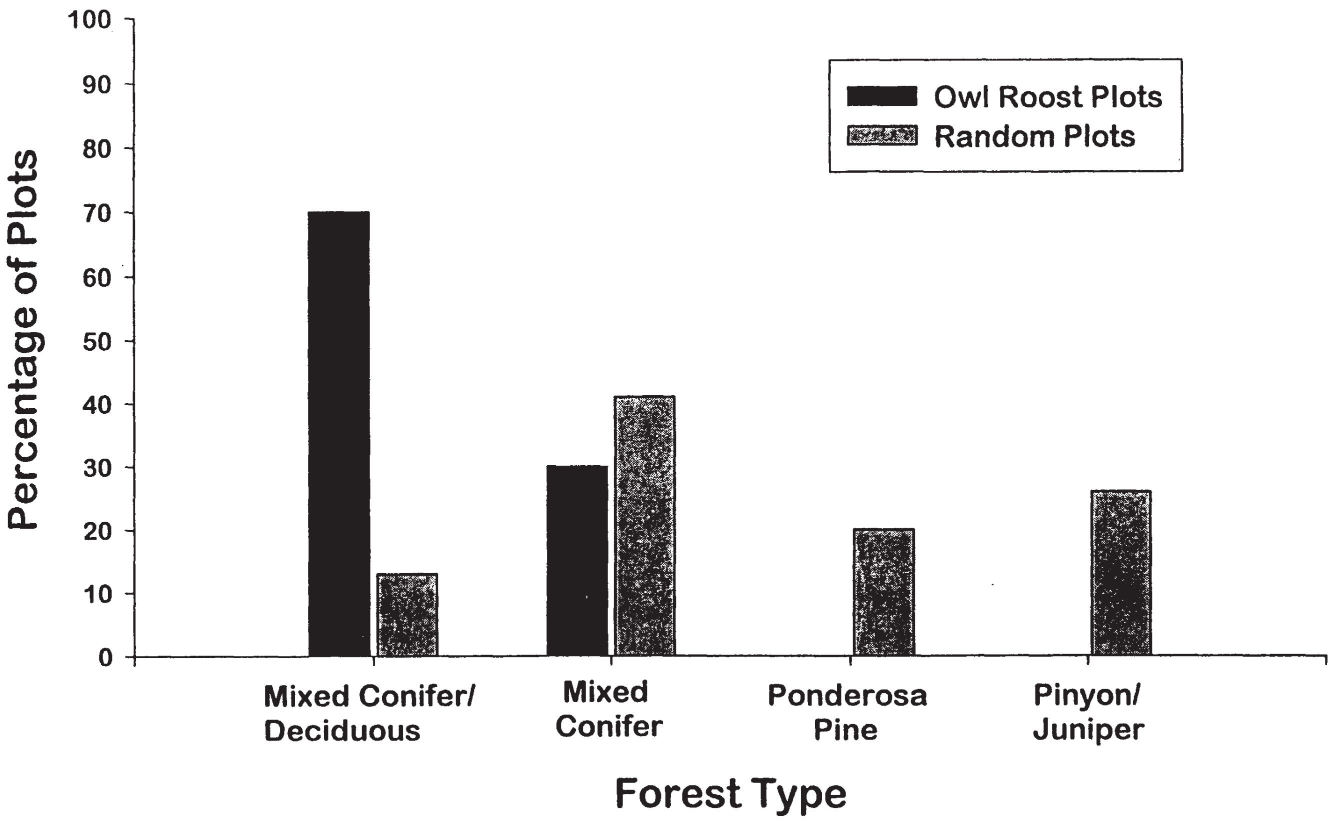

Figure 1—Distribution of Mexican spotted owl roost and randomly located sites among different forest association types in the San Mateo Mountains, Middle Rio Grande Basin, New Mexico.

Table 1—Basal areas of tree species in Mexican spotted owl roosting sites in the San Mateo Mountains, New Mexico (n = 64), compared with those in randomly selected plots within the owls' territories. Because the owls were never observed roosting in pinyon/juniper or ponderosa pine forests at our study area, we present two comparisons. First, random plots located in all forest association types in the territory (n = 69), and second, the subset of random plots that were located in forest types actually used by the owls for roosting (mixed conifer and deciduous, MC/D, and mixed conifer, MC; n = 36). Note that when the statistical influence of sample plots located in the unused forest types was removed, the difference between occupied roost sites and random plots in a higher basal area of Douglas-fir and southwestern white pine was no longer significant.

	Means ± SD		
Basal Area (m^2/ha)	Roost	Random Plots All Forest Types	MC/D, MC Forest Types
Douglas-fir	7.5 ± 6.5	3.9 ± /5.5**	6.9 ± 6.2
Southwestern White Pine	2.9 ± 6.3	0.8 ± 1.8**	1.4 ± 2.3
Pinyon/Juniper	0.2 ± 0.8	2.5 ± 4.5**	0.4 ± 1.9
Ponderosa Pine	2.9 ± 3.6	7.0 ± 7.2*	6.5 ± 5.9*
White Fir	0.6 ± 1.9	1.4 ± 4.2	2.7 ± 5.5*
Total Conifer Trees	14.2 ± 10.0	15.6 ± 8.7	18.0 ± 9.0
Gambel Oak and other Deciduous	5.5 ± 4.7	1.1 ± 2.0**	1.4 ± 2.4**
Total Live Tree	19.7 ± 9.8	16.9 ± 8.6	19.4 ± 8.9
Snags	1.8 ± 2.8	3.0 ± 4.8	4.1 ± 5.4

*,**. Statistically significant differences between occupied roost plots and random plots. Because of the large number of comparisons possible, the Bonferroni correction was used to set significance levels to * $p \leq 0.005$ and ** $p \leq 0.001$.

basal areas were no longer significant, and the only a greater basal area of Gambel oak and other deciduous species distinguished the occupied and random sites (table 1).

Deciduous trees also accounted for nearly three times more basal area in the roost sites than in either set of random plots, which were not different from one another: 52 percent of the total live tree basal area at roost sites versus 21 percent and 18 percent of total basal area in the random sites in all forest types and mixed-conifer or mixed-conifer/deciduous forest types, respectively.

Analysis of deciduous and coniferous tree densities in different D.B.H. classes showed significantly greater densities of small deciduous trees in the understory of roost plots, and significantly lower densities of conifers in the 15-30 cm D.B.H. class, than in either set of random plots. Surprisingly, the density of larger trees in roost plots was not significantly different from the surrounding forest matrix in either analysis. However, large deciduous and coniferous trees were only found in a few habitat plots so the power to detect a significant difference for the largest height and D.B.H. classes was low (power = 0.03-0.50). Snag densities in roost plots were only significantly different from random plots in the smallest height class (2-5 m, $p < 0.001$); these were primarily oak stems.

Discussion

Our results suggest that the habitat requirements of Mexican spotted owls may be more complicated that previously suspected. The territories of the owls in the southwest are large, often ranging from 250 to 1500 ha (USDI Fish and Wildlife Service 1995). At our study sites in both the San Mateo Mountains, as well as in the other mountain ranges, each owl territory contained 3-4 different forest types. As with most previous studies (Ganey and Balda 1994, Zwank and others 1994, Seamans and Gutièrrez 1995), we found that the birds roosted in the mixed-conifer or mixed-conifer/deciduous forest associations. No roost sites were located in pure ponderosa pine or pinyon/juniper woodlands. Like the prior studies, we also found that when we compared the characteristics of roost sites to random plots in all forest types, including those in the associations that were not used by the birds, roost sites had greater canopy closure, and greater density of Douglas-fir, southwestern white pine, Gambel oak and total live trees. But when tree species at roost sites were compared only to their availability in the used habitat types (mixed-conifer and mixed-conifer/deciduous forest types), the specific habitat characteristics important to spotted owls became even more pronounced. In this analysis, we found no significant difference in total live tree, total conifer, Douglas-fir or southwestern white pine density, or canopy closure. Roost sites and random sites in mixed conifer associations did not differ except that the occupied sites were most often in canyon bottoms or on the lower portion of slopes where there was a higher density of Gambel oak and other deciduous trees, and where deciduous trees in general made up over one-half (52 percent) of the total basal area of all live trees present. Although the detailed analysis of habitat use was conducted on only three owl territories, it is corroborated by the limited data from roost sites on 30 other territories in four mountain ranges in southwest New Mexico. In this larger sample, 84 percent of roosting areas were in canyon bottoms and contained deciduous trees.

The results of this analysis are similar to those of Rinkevich and Gutierrez (1996), who found that in Zion National Park owls occurred only in canyon bottoms with well-developed riparian vegetation, and of Johnson (1997), who found that owls in a number of different locations in Colorado always roosted in the narrow parts of canyon bottoms in areas of high canopy closure.

On the surface, our results appear to differ somewhat from those of several prior studies which have emphasized the importance of large diameter conifer trees in habitat selection (Ganey and Balda 1994, Zwank and others 1994, Seamans and Gutièrrez 1995). There are a number of reasons that may account for this. First, it is clear that the spotted owl has always occupied a number of different habitats types, including lowland bosques, and different aspects of the vegetation may be important in different parts of its range (see below). However, this study is one of the first to specifically include and quantify the basal area and densities of deciduous trees in roosting habitat, although others have noted the importance and prevalence of these species in spotted owl habitat (Ganey and others 1992, Ganey and Dick 1995, Seamans and Gutièrrez 1995, Tarango and others 1997). It also is the first to look at roost site selection only within used habitat types. Comparing roost plots to random plots throughout a study area often results in comparing roost plots in mixed-conifer forest to random plots that are located in pinyon/juniper or ponderosa pine forests. For example, approximately 30 percent of the random plots measured by Seamans and Gutièrrez (1995) at their study area in New Mexico, and 29 percent of the random plots measured in the present study, were in pinyon/juniper woodland. Only rarely have Mexican spotted owls been documented to utilize pinyon/juniper forest (Skaggs and Raitt 1988, Seamans and Gutièrrez 1995). Typical pinyon/juniper woodlands have tree cover of only 30-50 percent and the height of the tallest trees is usually only 4-8 meters (Moir and Carleton 1987). Therefore, due to the large statistical influence the unused random habitat plots may have on determining which variables are significant different among plots, it could be difficult to determine the *specific* habitat characteristics within the mixed-conifer habitat that actually affect habitat selection by the owls.

What all of these studies have in common is that they have found that Mexican spotted owls select roosting habitats are characterized by a high level structural complexity in the vegetation, just as they do in the other parts of the species range in California and the Northwest (Gutierrez and others 1995). In some parts of the southwest, this structure may be provided by old growth or mature mixed conifer forests, or by a well-developed understory of Gambel oak in ponderosa pine-oak woodlands. In many canyon habitats, however, deciduous vegetation, particularly riparian, may be the most important factor determining structural complexity. Mature montane riparian communities historically contained a wide variety of tree species, including Gamble and other oaks, cottonwoods, maples (*Acer grandidentatum*) and even conifer species such as Douglas-fir and white pine (Dick-Peddie 1993). Even today, remnant riparian habitats often contain a substantial component of Gambel oak that can provide vertical layering and vegetative structure for the birds.

Understanding the characteristics of suitable roosting habitat for spotted owls may be extremely important for a number of reasons. The birds are relatively "heat intolerant", and must find cool and shady places to roost during the summer (Barrows 1981). Intact riparian habitats, and other mature forests, are often substantially cooler than the surrounding areas. The owls simply may not be able to survive hot seasons in areas that do not have the appropriate thermal micro-environment. Spotted owls also sleep during much of the day, and during this period adult and particularly juvenile owls can be very vulnerable to diurnal and crepuscular avian predators, such as Northern goshawks (*Accipiter gentilis*) and great horned owls (*Bubo virginiana*). Typically, the owls roost in locations where multiple layers of vegetation make them difficult to detect, and they often perch on a horizontal branch next to a large tree trunk where a goshawk or great horned owl would run the risk of considerable injury if it attacked and missed its target (see also Buchanan and others 1995). Since caves and shaded sites near large cliffs can provide the same type of cool microhabitat and protection from aerial predators as do riparian areas, this may explain why the owls in our study always roosted in or near cliffs when they were not in the canyon bottoms.

As in the lowlands, canyon bottom riparian habitats in the mountains have undergone extensive alteration as a result of human activities. Many plant and animal species characteristic of this zone have become rare, and a number have been listed or been proposed for listing under the Endangered Species Act. While 88 percent of roost areas that we located, including all the canyon bottom sites, contained deciduous trees, Gambel's oak, a species found both in upland areas and canyon bottoms, was often the only deciduous species present in the immediate vicinity of roost sites. All of the canyons, however, had remnant cottonwoods and maples near the roost areas, indicating that these areas probably had more riparian characteristics before intensive grazing and other disturbances (Krueper 1993). Both our study and the results of earlier work suggest that within the mixed-conifer zone, spotted owls are selecting roost areas in canyon bottom microhabitats where deciduous trees offer the greatest vertical forest structure and canopy cover. Recognition of the canyon bottom habitat in the mixed-conifer zone as montane riparian, and monitoring of the effects of disturbance to this habitat (including grazing, road building and fire), may aid in the management of these sensitive areas. The apparent importance of deciduous vegetation in the roosting habitat selection of Mexican spotted owls suggests that the decline of montane riparian areas may have an even greater effect on biological diversity in the southwest than was originally suspected.

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