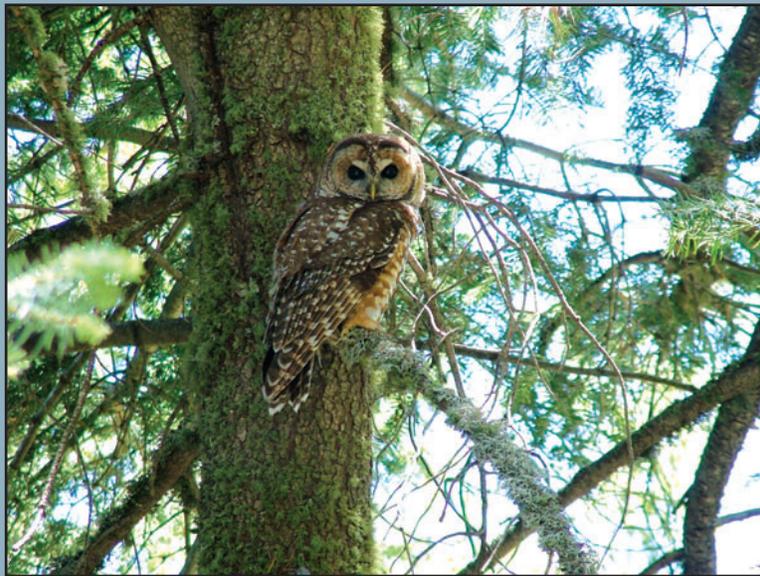


Status and Ecology of Mexican Spotted Owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico

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Abstract

This report summarizes current knowledge on the status and ecology of the Mexican spotted owl within the Upper Gila Mountains Recovery Unit (UGM RU). It was written at the request of U.S. Forest Service personnel involved in the Four Forests Restoration Initiative (4FRI), a collaborative, landscape-scale restoration effort covering approximately 2.4 million ac (1 million ha) across all or part of four National Forests (Apache-Sitgreaves, Coconino, Kaibab, and Tonto National Forests) located within the UGM RU. The UGM RU supports >50% of the known population of Mexican spotted owls, and the central location of the UGM RU within the overall range of the owl appears to facilitate gene flow throughout that range. Consequently, the UGM population is viewed as important to stability within the overall range of the owl, and management that impacts owls within the UGM RU could affect owl populations beyond that RU.

Keywords: abundance, demography, habitat selection, diet composition, movements

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Cover: Roosting Mexican spotted owls in mixed-conifer forest (top) and ponderosa pine–Gambel oak forest (bottom). These are the primary forest types occupied within the Upper Gila Mountains Recovery Unit. Top photo by Craig P. Wilcox, Coronado National Forest.

Executive Summary

This report summarizes current knowledge on the status and ecology of the Mexican spotted owl within the Upper Gila Mountains Recovery Unit (UGM RU). It was written at the request of U.S. Forest Service (USFS) personnel involved in the Four Forests Restoration Initiative (4FRI), a collaborative effort (led by USFS personnel and featuring broad public outreach) to restore ponderosa pine dominated forest ecosystems covering approximately 2.4 million ac (1 million ha) across all or part of four National Forests (Apache-Sitgreaves, Coconino, Kaibab, and Tonto National Forests) located within the UGM RU.

The UGM RU supports >50% of the known population of Mexican spotted owls. Habitat connectivity within the UGM RU is high relative to other RUs, allowing high levels of owl movements and gene flow, and the central location of the UGM RU within the overall range of the owl appears to facilitate gene flow throughout that range. Consequently, the UGM population is viewed as important to stability within the overall range of the owl, and management that impacts owls within the UGM RU could affect owl populations beyond that RU.

We have little information on historical distribution of Mexican spotted owls within the RU. This owl currently is distributed widely in mountains and canyons featuring mixed-conifer, ponderosa pine–Gambel oak, and/or riparian forests. In other parts of the range, they occur in rocky canyons lacking extensive forest cover, but this appears atypical within the UGM RU.

Mexican spotted owls in the UGM RU occupy large (up to 2,500 ac [1,012 ha]) home ranges. They typically concentrate use in smaller portions of this larger home range, with these “activity centers” typically comprising <50% of home-range area. Most radio-marked owls remain near their breeding areas year-round, but some migrate during winter. This migration, which has been observed in all populations studied, typically entails movement to lower elevations. Resident owls greatly expand their home range during the non-breeding season, but areas used during the breeding and non-breeding seasons overlap spatially. Thus, protection of breeding-season home ranges protects habitat that is used throughout the year.

All studies in the UGM RU indicate that home ranges are located in areas containing greater amounts of mature forest than surrounding areas, or sometimes in areas of younger forest containing relatively large trees (>18 in [45.7 cm] diameter at breast height [dbh]). Differences between owl home ranges and randomly located areas are most pronounced near the nest area and decline as areas farther from nests and range centers are included.

Mexican spotted owls appear to be more selective for habitat used for roosting and nesting than for habitat used for foraging. Most owls roost and nest in mixed-conifer forest, followed by ponderosa pine–Gambel oak forest. Ponderosa pine and riparian forest are used less often and other cover types are used rarely for roosting and nesting. Roost and nest areas typically feature high basal area ($\geq 85 \text{ ft}^2 \text{ ac}^{-1}$), high canopy cover ($\geq 50\%$), and large trees. A prominent hardwood component frequently is present, adding complexity and a layering effect to forest structure. Where these types of forests are present to provide nesting and roosting habitat, owls appear to be able to forage in a wider variety of forest and woodland types and forest structural conditions.

We lack long-term data on how high-severity wildland fire affects spotted owls, but short-term studies indicate that many burned areas continue to be used. We also lack information on the specific effects of other disturbance factors such as grazing, tree harvest, urbanization, and climate change on owls and their habitat.

Mexican spotted owls within the UGM RU exhibit low and variable reproduction, low juvenile survival, and relatively high ($>75\%$) adult survival. We have little information on limiting factors, or on how factors such as weather and habitat influence owl vital rates. We have no current information on population trend, but all populations studied within the RU during the 1990s ($n = 5$) appeared to be declining during that period.

Mexican spotted owls eat a wide variety of prey, and diet composition varies among geographic areas and/or cover types. Five types of nocturnally active small mammals (woodrats, white-footed mice, voles, rabbits, and pocket gophers) typically comprise $>65\%$ of prey biomass in this RU. Links between owl reproduction and prey abundance suggest that overall prey biomass is more important than abundance of any single species or group. These small mammals each have unique habitat relationships, suggesting that managing for a diversity of habitat conditions may best maximize prey abundance and diversity. Retention of slash, large trees, snags, and logs may benefit species such as woodrats, whereas voles and pocket gophers likely will respond positively to management for increased herbaceous understory cover, height, and diversity.

We generally know little about ecological relationships between Mexican spotted owls and their potential predators and competitors. Spotted owl home ranges overlap considerably with those of great horned owls in some areas. Diet composition is similar between these owls in these areas of spatial overlap, but patterns of habitat use within the home range differ. Mexican spotted owls concentrated activity in forests with $>40\%$ canopy cover, whereas great horned owls concentrated activity

in forests with <40% canopy cover. Thus, these owls appear able to partition habitats where they co-occur, but competitive relationships could be altered by forest management that reduces canopy cover across much of the landscape.

We summarize the results of three efforts to model and map Mexican spotted owl habitat within the UGM RU, because all yielded products and insight that may be useful to 4FRI planners. We also summarize current knowledge on effects of human disturbance on owls, and on seasonal movements, landscape connectivity, and genetic structure within the overall owl population.

Many information gaps remain. We discuss two related gaps that appear important in the context of 4FRI: the lack of data on structural conditions and spatial extent of habitats used by Mexican spotted owls prior to effective fire suppression, and the lack of data on how forest management activities affect spotted owls and their prey and habitat. We suggest that the landscape-scale restoration effort represented by 4FRI provides a unique opportunity to address those information gaps by incorporating owl habitat considerations in landscape designs and monitoring owl response to forest treatments. We suggest some potential management thresholds that could be used in designing treatments, based on studies of owl habitat use. Given the threatened status of this owl, and the importance of the UGM RU population to overall population connectivity, we urge managers to proceed cautiously.

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Introduction

This report summarizes current knowledge on the status and ecology of the Mexican spotted owl (scientific names of species cited in text are provided in Appendix 1) within the Upper Gila Mountains (hereafter UGM) Recovery Unit, one of six geographic subdivisions (Recovery Units, hereafter RUs) recognized within the US range of this owl (fig. 1; USDI FWS 1995). The Mexican spotted owl, one of three recognized subspecies (fig. 2) of spotted owls (AOU 1957), was listed in 1993 as a threatened species under the Endangered Species Act of 1973, as amended (ESA; 16 U.S.C. 1531).

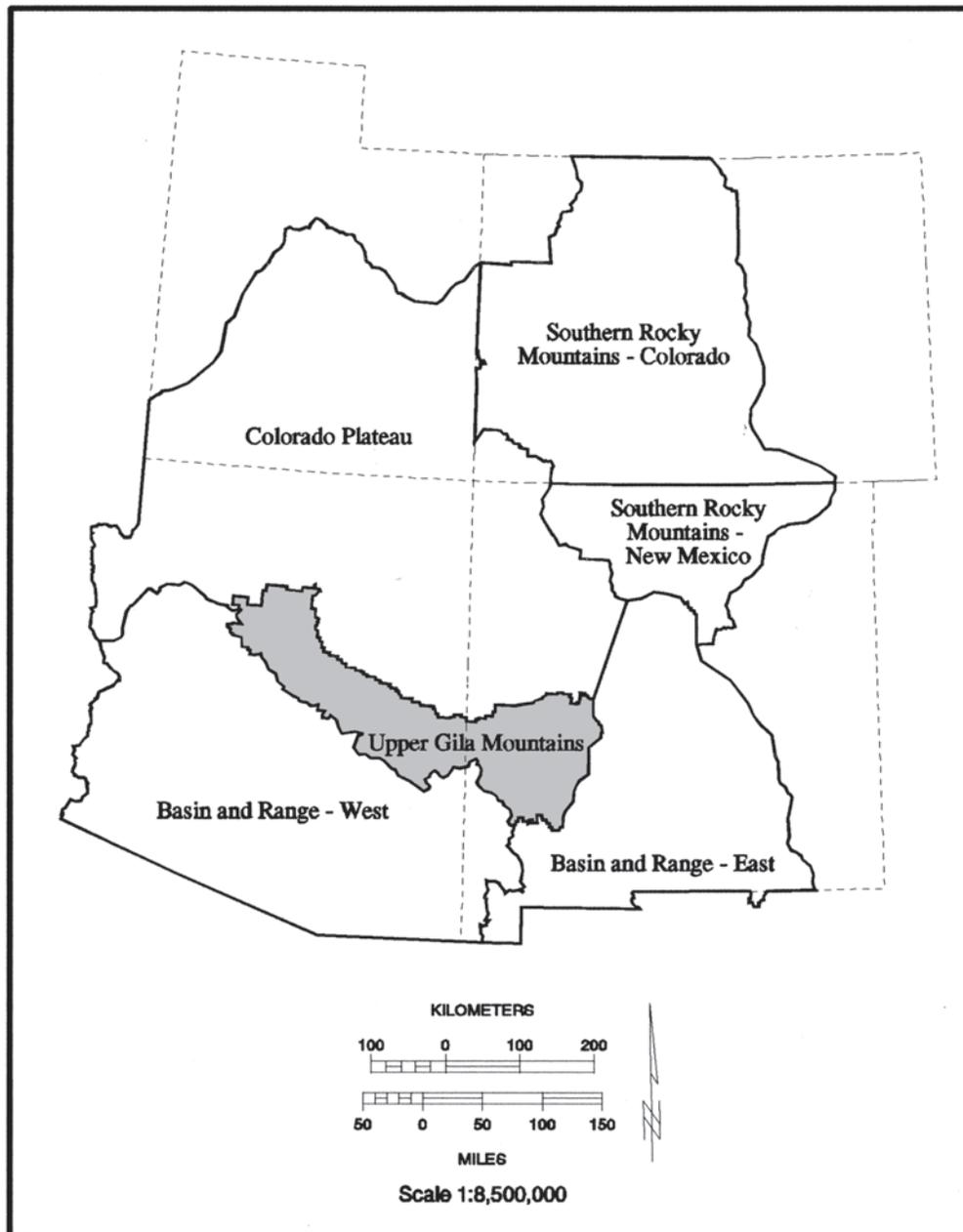


Figure 1. Recovery Units within the United States recognized in the Mexican spotted owl recovery plan (USDI FWS 1995).



Figure 2. Range map of three subspecies of spotted owls (from Ward [2001], modified from Gutiérrez and others [1995: Figure 1]).

This report was undertaken at the request of U.S. Forest Service (USFS) personnel involved in the Four Forests Restoration Initiative (hereafter 4FRI). 4FRI is a collaborative effort to restore ponderosa pine dominated forest ecosystems covering approximately 2.4 million ac (1 million ha) across all or part of four National Forests (Apache-Sitgreaves, Coconino, Kaibab, and Tonto National Forests) in Arizona (fig. 3). This effort is led by USFS personnel but also solicits input and participation from a diverse group of stakeholders. Mexican spotted owls are widely distributed throughout this region (see below). Because of the scale of the 4FRI effort, the widespread treatments proposed could have broad effects, either positive or negative, on this threatened owl and its habitat. Consequently, planners involved with 4FRI recognized a need to consider carefully the status and ecology of this threatened owl in planning and implementing landscape-scale treatments.

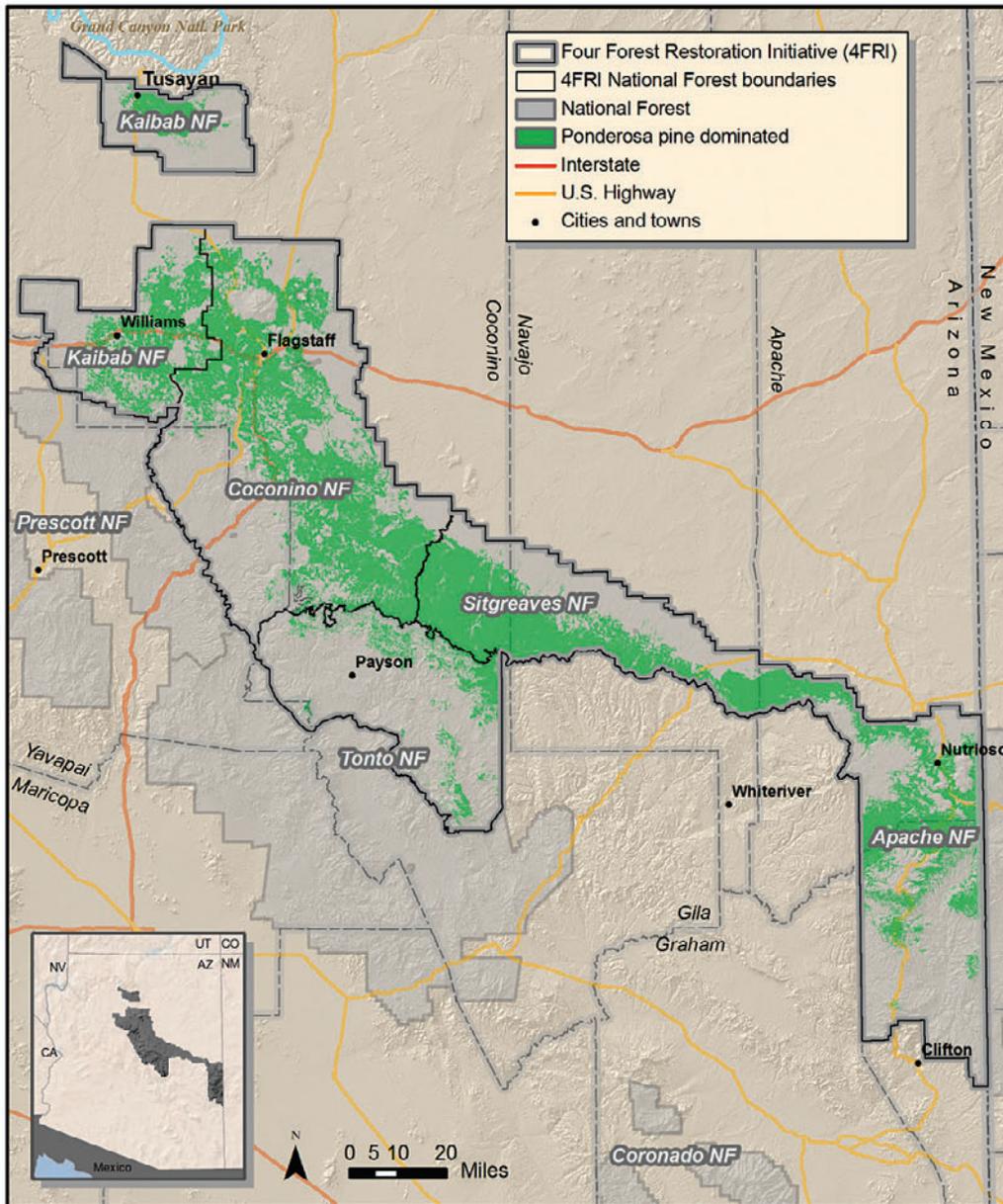


Figure 3. Map of the area covered by the Four Forests Restoration Initiative (4FRI), a collaborative effort to restore ponderosa pine dominated forest ecosystems on portions of four national forests (Apache-Sitgreaves, Coconino, Kaibab and Tonto) along the Mogollon Rim in Northern Arizona. Map created by Jill Rundall, Lab of Landscape Ecology and Conservation Biology, The ForestERA Project. Used by permission.

This report was prepared to summarize and synthesize existing knowledge on status and ecology of Mexican spotted owls in this region. The intent is to aid planners in evaluating potential benefits or impacts of management actions for spotted owls and their habitat. Because USDI FWS (1995) organized information by RUs, because 4FRI includes a large portion of the UGM RU, and because initial treatments will occur within the UGM RU, 4FRI personnel requested that the geographic scope of this report be expanded to include the entire RU, which also incorporates major portions of the Gila and Cibola National Forests in New Mexico.

This report is intended to be an overview of biological characteristics and ecological relationships of this subspecies relevant to forest planning efforts. It is not intended to be exhaustive, but rather to summarize and synthesize the information most relevant to resource managers and planners in a reasonably concise format. As such, we do not summarize all aspects of basic natural history here, but instead refer readers interested in spotted owl natural history to reviews in Gutiérrez and others (1995) and USDI FWS (1995). We emphasize owl and prey habitat in this report, as habitat is what will be directly manipulated in forest treatments under 4FRI. We use English units for parameters such as length, diameter, area, and basal area, because those are the units used by the land managers that comprise our primary target audience. In all cases, we either provide metric equivalents or (in tables) conversion factors to allow readers to convert English units to metric units.

Where data exist specific to the UGM RU, we rely primarily on those data. We supplement those data with results from outside the UGM RU where data specific to that RU are lacking. Because landscape-scale conservation planning requires the best available data, we rely primarily on data from published, peer-reviewed sources and generally delve into unpublished reports only where such data are lacking. Most published information on Mexican spotted owls within the UGM RU derives from a relatively small number of studies and study areas. Some of these studies were highly productive and contributed to a large number of papers. To aid readers in understanding which papers were derived from which study areas, we provide a list of study areas, primary study objectives, and resulting products in Appendix 2.

The Upper Gila Mountains Recovery Unit

The UGM RU (fig. 1) is based primarily on the Upper Gila Mountains Forest Province (Bailey 1980), but it also includes the southern end of the Colorado Plateau Ecoregion. Williams (1986) called this area the Datil-Mogollon Section, part of a physiographic subdivision transitional between the Basin and Range and Colorado Plateau Provinces. This complex area consists of steep mountains and deep, entrenched river drainages dissecting high plateaus. The Mogollon Rim, a prominent fault scarp, bisects the UGM RU.

McLaughlin (1986) described a “Mogollon” floral element in this region. The vegetation ranges from grasslands at lower elevations through pinyon-juniper woodlands, ponderosa pine, mixed-conifer, and spruce-fir forests at higher elevations. Mixed-conifer forests are defined in this report as forests dominated by mixtures of Douglas-fir, white fir, ponderosa pine, and sometimes limber or southwestern white pine (Brown and others 1980; see also Appendix 3). Many canyons contain stringers of deciduous riparian forests, particularly at elevations below 8,000 ft (2,440 m). The UGM RU contains the largest contiguous ponderosa pine forest in North America, an unbroken band of forest 25 to 40 mi (40 to 64 km) wide and approximately 300 mi (483 km) long extending from north-central Arizona to west-central New Mexico (Cooper 1960).

Federal lands, mostly USFS, encompass 67% of the UGM RU (fig. 4; USDI FWS 1995). Tribal lands account for 17%, privately owned lands 12%, and State lands (Arizona and New Mexico) 4% of the RU (USDI FWS 1995). Major land uses and management objectives within the UGM RU include commercial timber harvest, fuels reduction, ecological restoration, livestock production, management for water quantity and quality, and recreation. Fuelwood harvest, for both personal and commercial use, occurs across much of the UGM RU. Livestock grazing is common on USFS lands and large portions of the Fort Apache and San Carlos Indian Reservations. Recreational activities such as hiking, camping, hunting, and fishing also attract many people to this RU, and many people from lower elevations across Arizona come to this area to experience the shade, cooler summer temperatures, and fall colors provided by these forests, or for winter snowplay.

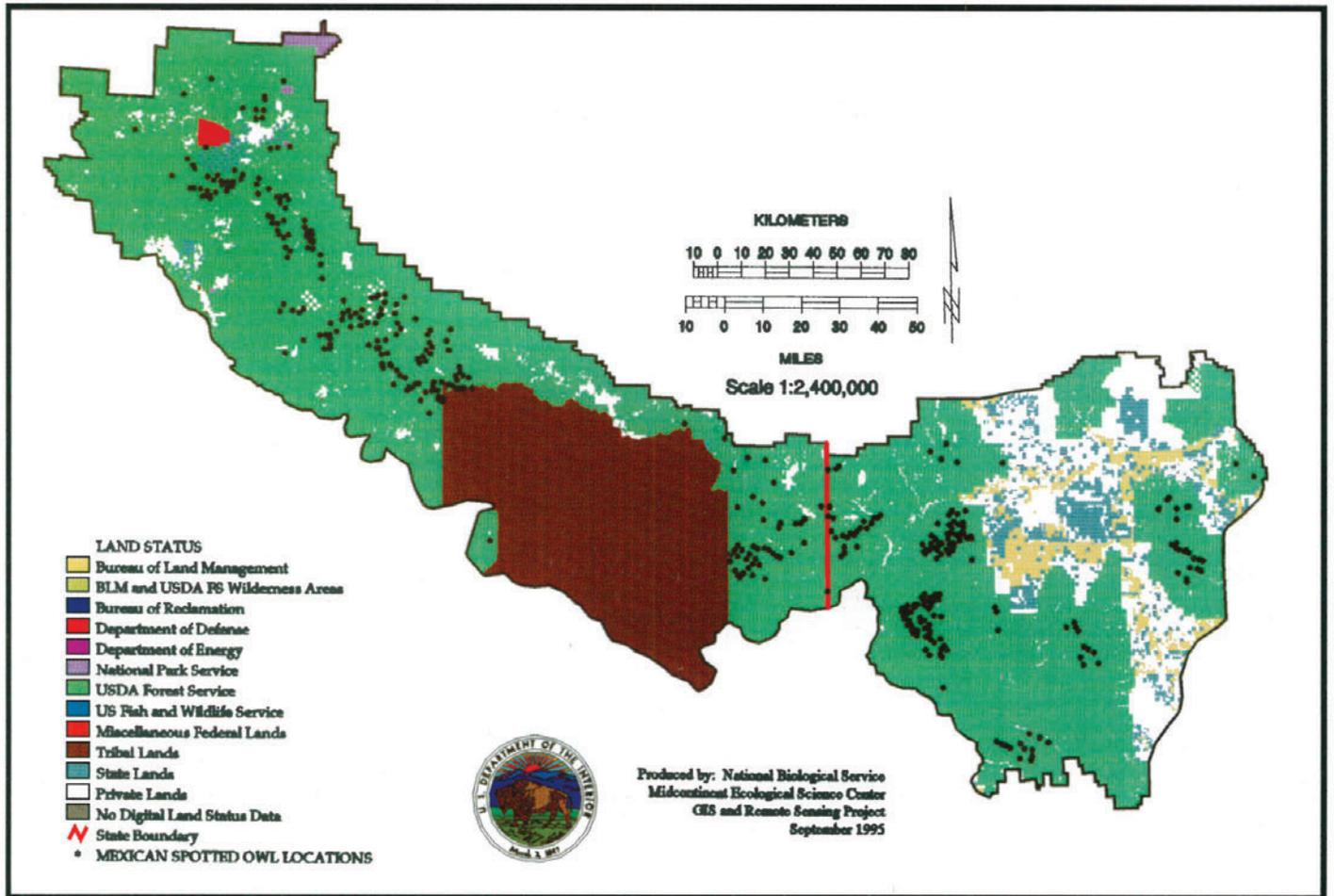


Figure 4. Land ownership and Mexican spotted owl site locations in the Upper Gila Mountains Recovery Unit (from USDI FWS 1995: Figure II.B.6). Note the widespread distribution of owls within the RU, as well as the concentration of owls on National Forest System lands. Location data were not available for tribal lands. Although this map is 15 years old, the patterns shown remain valid.

Distribution

The Mexican spotted owl occurs in forested mountains and rocky canyonlands, ranging from Utah, Colorado, Arizona, New Mexico, and the western portions of Texas south into several States of Mexico (fig. 2; Gutiérrez and others 1995, Ward and others 1995). This owl does not occur uniformly throughout this broad geographic area, but instead occurs in disjunct areas that correspond with isolated mountain ranges and canyon systems (fig. 5; Ward and others 1995).

Historical information on Mexican spotted owls throughout their range is sparse and anecdotal but clearly documents that these owls were present in the UGM RU. For example, Ligon (1926:422) reported numerous observations of spotted owls in “the San Mateo Mountains, Black Range and Mogollon Mountains and in corresponding latitudes in eastern Arizona” (presumably indicating the Blue Range Primitive Area and White Mountains of eastern Arizona). Bailey (1928; see also Steele 1927) also lists several locations where spotted owls were observed in this general region. Ligon (1926:422) stated that these owls were “...by no means as scarce in favored sections of their range as one unfamiliar with their habits might believe.”

Historical data for the western portion of the RU are sparse. Huey (1930) collected an adult female spotted owl in June 1929 near Little Spring, at the base of the San Francisco Peaks. This is the only published record we are aware of for the western UGM RU prior to 1970. However, this location falls toward the western edge of the RU, suggesting that spotted owls historically were distributed throughout the RU. Thus, historical data document that spotted owls were present, and likely not extremely rare, in the eastern portion of the UGM RU, and also present towards the western end of the RU. Beyond this, little is known about historical distribution of this owl within the UGM RU.

Because of its threatened status and the association between spotted owls and older forests, considerable attention has focused on this owl since 1989 (USDA FS 1990). As a result, we know far more about current distribution than we do about historical distribution. Within the UGM RU, Mexican spotted owls are widely distributed (fig. 5), with most occurring on National Forest System lands (fig. 4; see also USDI FWS 1995, Ward and others 1995). They have been located on all six National Forests within this RU. Spotted owls also occur on tribal lands within this RU, but we do not have access to data on numbers and specific locations of owls occupying these lands.

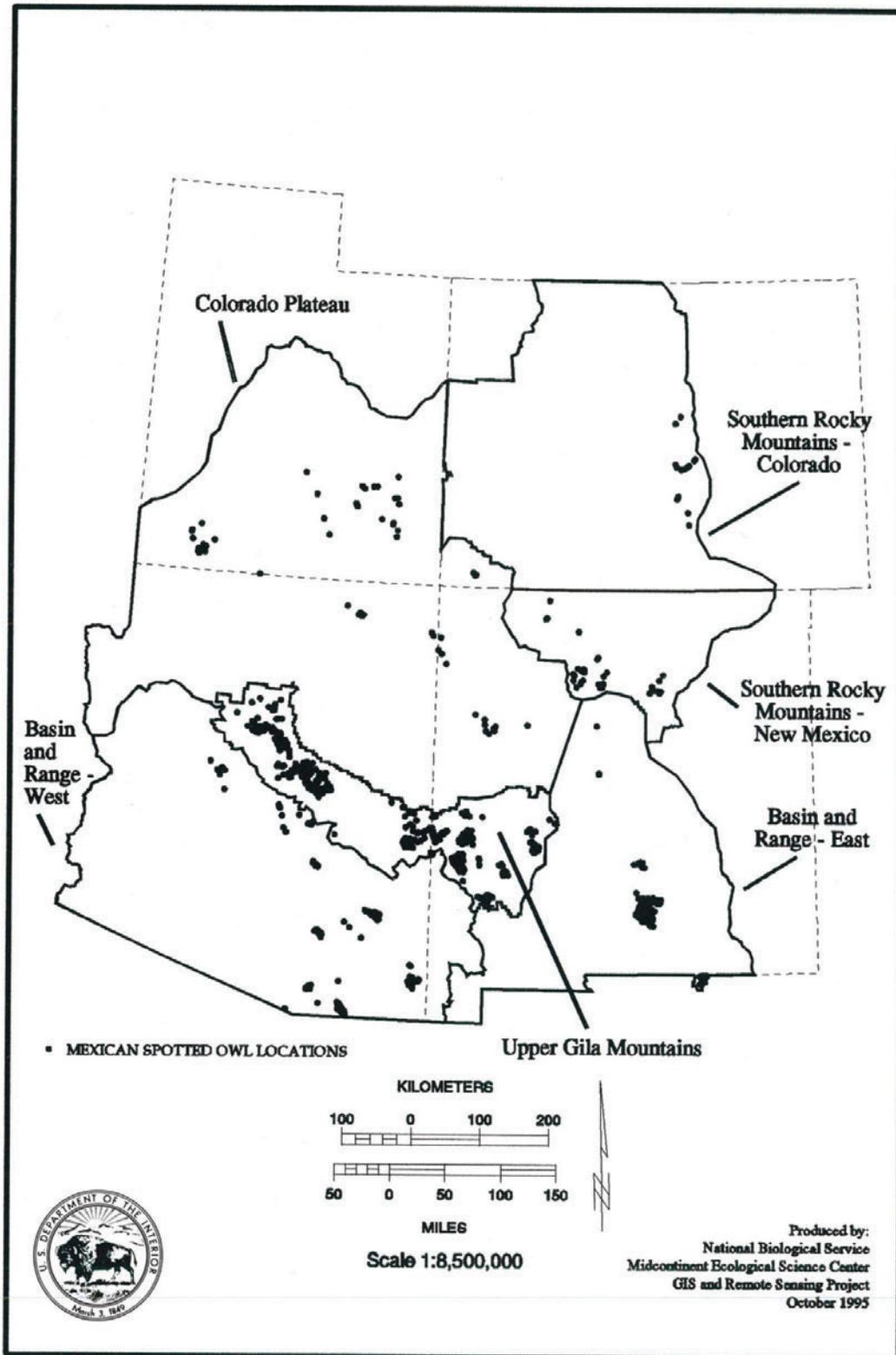


Figure 5. General areas occupied by Mexican spotted owls within their range in the United States (from USDI FWS 1995: Figure II.A.2). Note the patchy distribution of owls throughout much of the range, contrasted with the relatively continuous distribution throughout the Upper Gila Mountain Recovery Unit. The apparent gap in the center of that Recovery Unit is due to lack of location data from tribal lands. Location data were not available for tribal lands. Although this map is 15 years old, the patterns shown remain valid.

Abundance

Knowledge of abundance is useful in managing for threatened species. Although the total number of Mexican spotted owls occupying the UGM RU is unknown, Ganey and others (2004) estimated abundance of territorial owls in this RU based on mark-recapture sampling of owls in a stratified-random set of 25 quadrats (ranging in size from 27.2 to 47.5 mi² [43.7 to 76.4 km²]) across the UGM RU (fig. 6). They estimated that 2,941 territorial adult or subadult owls occupied this RU (excluding tribal lands, which were not included in the sampling frame). This estimate, although based on rigorous methods, was imprecise, with a 95% confidence interval ranging from 833–5,049 owls.

No similar estimates are available for other RUs, but agency surveys for Mexican spotted owls provide a source of relative abundance data across the range of the owl. Since 1989, when USFS began using standardized procedures to identify and record “sites” (as defined in USDI FWS 1995) occupied by spotted owls, a cumulative total of 424 such sites have been documented in the UGM RU (USDI FWS 1995). This constitutes 55.9% of the known spotted owl sites documented range-wide (USDI FWS 1995). It is not possible to estimate abundance directly from these data, however, for the following reasons: these sites may indicate occupancy by either a single owl or a pair of owls, it is not known how many of these sites are occupied during any given year, and these surveys may not be effective at locating non-territorial individuals (referred to as “floaters,” discussed below).

These known owl sites are well distributed among the National Forests comprising this RU, with the exception of the Kaibab National Forest, which has few known owl sites (fig. 7). The UGM RU contains the two forests with the greatest number of known sites and three of the four top forests in terms of numbers of known sites (fig. 7). Thus, available data suggest both high relative abundance and widespread distribution in this RU. Note that both abundance and distribution are underestimated due to lack of data from tribal lands.

Owl Density

Estimates of owl density, or the number of individuals in a population divided by the area used by that population, also can be useful in understanding owl abundance and distribution patterns. Only one study (Ganey and others 2004) estimated density of Mexican spotted owls within the UGM RU while accounting for imperfect detection of owls. That study was geographically extensive but was limited to a single year. Density of adult and subadult owls within individual quadrats in this study ranged from 0 to 1.14 territorial owls mi⁻² (0 to 0.44 owls km⁻²). Density in this study was highly correlated with an index of topographic roughness, with greater densities of owls in quadrats characterized by rugged topography.

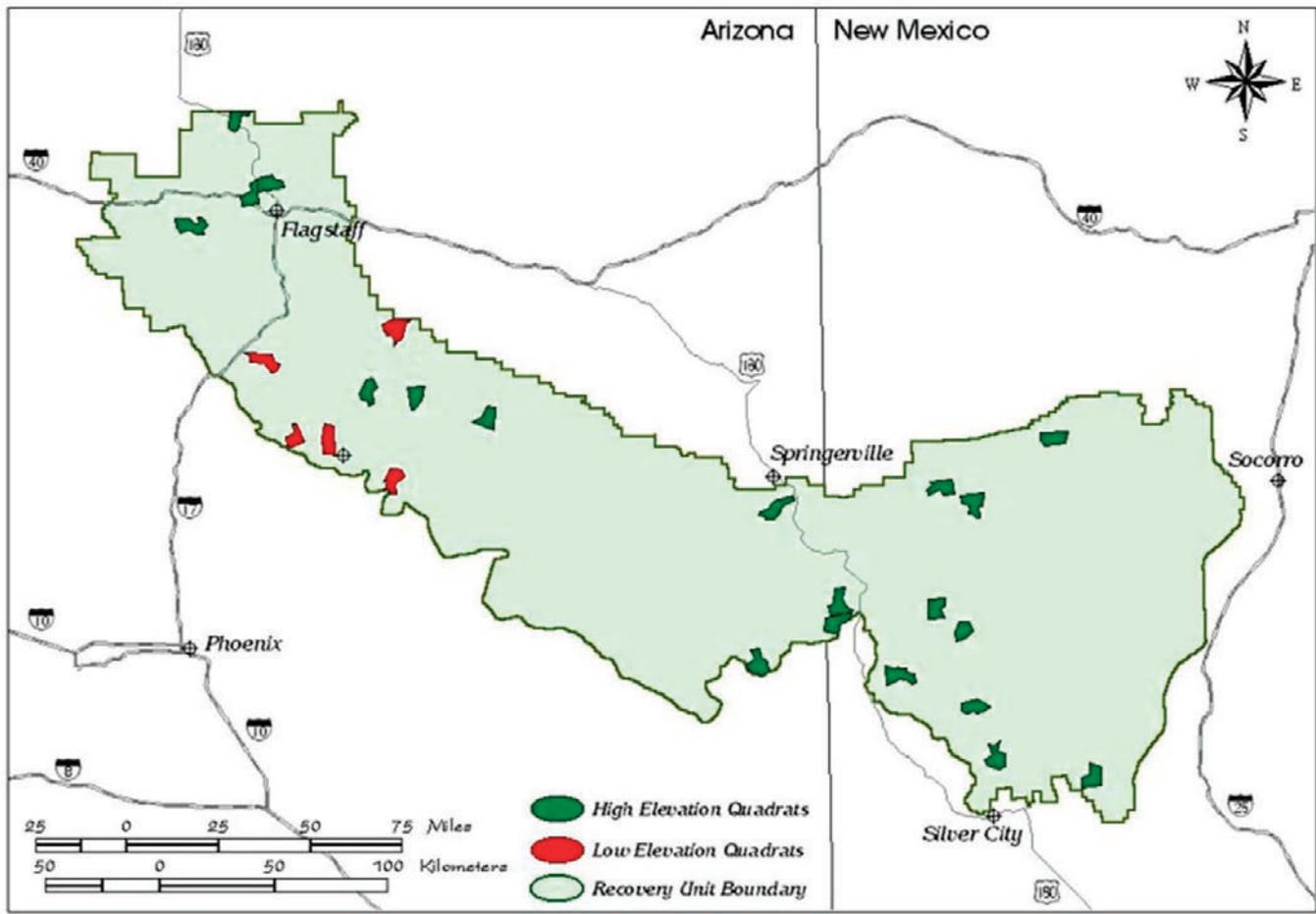


Figure 6. Sample quadrats included in a study of abundance of Mexican spotted owls, Upper Gila Mountains Recovery Unit, Arizona and New Mexico (Ganey and others 2004).

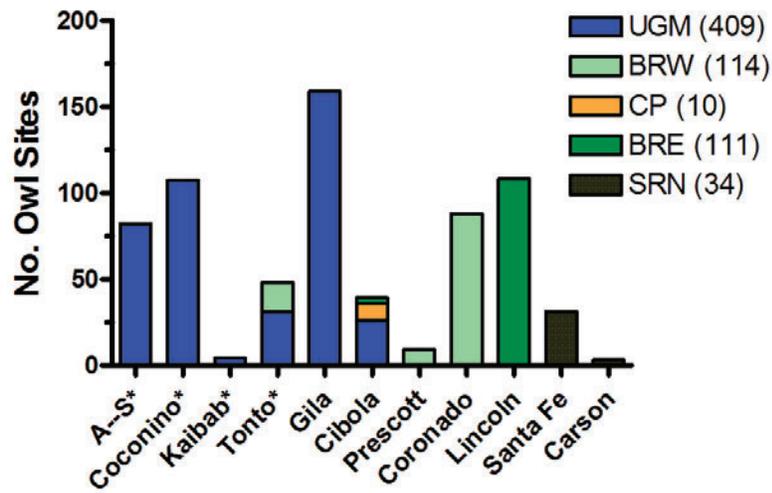


Figure 7. Numbers of known owl sites by National Forest within the Southwestern Region, US Forest Service, from USDI FWS (1995). Forests contained within the 4FRI analysis area are arrayed on the left and identified by an asterisk. Note that figure shows only sites within the Southwestern Region, USFS (Arizona and New Mexico). Consequently, sites in several Recovery Units that fall largely outside of those states are underestimated. A/S = Apache-Sitgreaves National Forest. Although these data are 15 years old, the patterns shown remain largely unchanged.

Seamans and others (1999) reported annual observed densities of territorial owls over a five-year period from two mark-recapture study areas (CNF and GNF, described in Appendix 2) in Arizona and New Mexico. Density in these areas ranged from 0.135 to 0.389 and from 0.285 to 0.466 owls mi^{-2} (0.052 to 0.150 and 0.110 to 0.180 owls km^{-2}) across years (calculated from data in Seamans and others 1999: fig. 5). Density in both study areas was related directly to fecundity (an index of reproductive output) from two years prior to each density estimate (in other words, higher fecundity results in greater density two years later; Seamans and others 1999). Density was consistently greater in the New Mexico population during this period, and Seamans and others (1999) suggested that this reflected habitat conditions. The New Mexico study area contained greater amounts of mixed-conifer forest than the Arizona study area (28.5 vs. 14.4% of total area), a forest type commonly occupied by Mexican spotted owls (see below). In contrast, the study area in Arizona was dominated by ponderosa pine–Gambel oak forest (82.2%) and contained little mixed-conifer forest.

Thus, three ecological factors have been associated with Mexican spotted owl density: topographic relief, fecundity in previous years, and vegetation composition. The relative influence of these factors is unknown, and they may not act independently. Furthermore, although relative density among various forest-cover types or other categories is of interest, density alone can be a misleading indicator of habitat quality (Van Horne 1983). For example, Seamans and others (1999) reported greater density in their New Mexico study area than in their Arizona study area, yet demographic rates were greater in the Arizona study area (see below). Consequently, it is important to assess demographic parameters such as survival, reproduction, or especially rate of population change when attempting to define habitat quality.

Home Range Size and Space Use

Understanding the spatial requirements of Mexican spotted owls and factors that influence those requirements can aid in designing conservation strategies. Four concepts relevant to understanding space use by resident Mexican spotted owls are discussed below. These are: territory, home range, activity center, and core area.

Territory

A territory is defined as an exclusive area defended by the occupant (Welty 1975:224-225). Spotted owls are described as territorial in the sense that mated pairs defend a breeding territory, at least during the nesting season. Seasonal and longer-term fidelity to these territories often is great in Mexican spotted owls, with many owls remaining on the same territory year after year (Gutiérrez and others 1995). No direct estimates of territory size are available for Mexican spotted owls within the UGM RU, but estimates of nearest-neighbor distances between adjacent pairs may provide insight into the size of exclusive areas used by this owl.

Such estimates are available for two study areas where there is reasonable certainty that all pairs of owls in a given area were located. Mean distances between adjacent pairs in these areas were 1.3 mi (2.1 km) in New Mexico ($n = 31$ pairs; Peery and others 1999; GNF in Appendix 2) and 1.5 mi (2.4 km) in Arizona ($n = 42$ pairs; May and Gutiérrez 2002; CNF in Appendix 2), suggesting that exclusive use areas average approximately 855 to 1115 ac (346 to 452 ha), respectively.

Home Range

A home range is defined as the area used by an animal during its normal activities (Burt 1943) and represents the spatial area in which resident owls attain all of their life requisites within a defined time period. Unlike territories, home ranges of adjacent pairs may overlap spatially, and the entire home range typically is not defended. Home ranges typically are assumed to be larger than territories, although few studies have formally evaluated differences between territories and home ranges. In a recent study, Anich and others (2009) found that territories of Swainson's warblers (defined based on locations where radio-marked warblers were observed singing) were on average 70% as large as home ranges defined by movements of those radio-marked warblers.

Investigators have studied home-range size of Mexican spotted owls within the UGM RU directly by monitoring movements of radio-marked owls in four study areas (Table 1). Home-range size varied considerably among study areas, but the factors underlying that variation are unclear. Sampling regimes and sample sizes varied among studies, and studies were conducted in different years. All of these factors can influence estimates of home-range size (Kernohan and others 2001), making direct comparisons among studies difficult. Consequently, observed differences among studies could be due to differences in methodology, local habitat quality including abundance of prey, biogeographic effects (for example, differences in climate pattern or biogeographic region), temporal variation (studies conducted in different years), or all of the above. There is evidence from other areas that local habitat composition (Ganey and others 2005) and/or prey abundance (Carey and others 1992, Zabel and others 1995) can influence home-range size of spotted owls, but similar information is lacking for the UGM RU.

Only one study within the UGM RU estimated size of seasonal home ranges (Ganey and others 1999). Range size more than doubled from the breeding to the non-breeding season in this study (Table 2).

Activity Centers and Core Areas

An activity center is an area within the home range receiving concentrated use. A core area is a specific type of activity center that usually includes a minimum area for protecting special resources like trees and groves used for roosting, nesting, or rearing of young (Bingham and Noon 1992, Ward and Salas 2000).

Table 1. Area of annual home ranges or activity centers of radio-marked Mexican spotted owl pairs and individuals in the Upper Gila Mountains Recovery Unit. *N* = number of pairs or individual owls included in estimates. Home range estimates based on the 95% adaptive kernel estimator; activity centers based on the 75% adaptive kernel estimator. Data from Ganey and Dick (1995: tables 4.2 and 4.3) and Ganey and others (1999). Activity-center area was estimated only for radio-marked pairs of owls.

Study area ²	<i>N</i>	Home-range area ¹		Activity-center area ¹		% of home range ³
		Mean	<i>SD</i>	Mean	<i>SD</i>	
Pair home ranges						
SFP	2	2204	124	872	344	39.6
WC	1	699		287		41.1
BMC	7	2464	1218	872	450	35.4
Individual home ranges						
SFP	4	2187	517			
WC	2	647	198			
WM	2	1310	400			
BMC	14 ⁴	2212	295			

¹ Area (acres, mean and standard deviation [*SD*]). To convert home-range size to ha, divide by 2.47.

² Acronyms for study areas: SFP = San Francisco Peaks, WC = Walnut Canyon, BMC = Bar-M Canyon, and WM = White Mountains. All study areas were in Arizona, and all except WM (Apache-Sitgreaves National Forest) were within the Coconino National Forest. Study areas are described further in Appendix 2.

³ Percent of overall home range contained within the activity center, calculated from table values as: (Activity-center area/Home-range area) * 100.

⁴ Fourteen range estimates computed for 13 individual owls. One radio-marked female dispersed to a new territory during the study. Separate range estimates were computed for this owl in different years.

Table 2. Area of home ranges or activity centers of radio-marked Mexican spotted owl pairs and individuals in ponderosa pine–Gambel oak forest during the breeding and non-breeding seasons. Data from Ganey and others 1999: Table 1. *N* = number of owl pairs or individual owls included in estimates. Home range estimates based on the 95% adaptive kernel estimator; activity centers based on the 75% adaptive kernel estimator.

Parameter	Breeding season ¹			Non-breeding season ¹		
	<i>N</i>	Mean	<i>SE</i>	<i>N</i>	Mean	<i>SE</i>
Owl pairs						
Home-range area ²	4	1303	214	7	2772	420
Activity-center area ²	4	319	40	7	981	200
% of home range ³	4	24.5		7	35.4	
Individual owls						
Home-range area ²	8	971	173	14 ⁴	2345	363
Activity-center area ²	8	302	54	14 ⁴	808	133
% of home range ³	8	31.1		14 ⁴	34.5	

¹ Seasons: Breeding = 1 Mar–30 Aug, Non-breeding = 1 Sep–28 Feb.

² Area (acres; mean and standard error [*SE*]). To convert home-range or activity-center size to ha, divide by 2.47.

³ Percent of seasonal home range contained within the activity center, calculated from table values as: (Activity-center area/Home-range area) * 100.

⁴ Fourteen range estimates computed for 13 individual owls. One radio-marked female dispersed to a new territory during the study. Separate range estimates were computed for this owl in different years.

Activity centers and core areas have been used to estimate the size of areas needed to protect habitat most commonly used by spotted owls (for example, Bingham and Noon 1992, USDI FWS 1995).

Estimates of annual activity-center size were available for radio-marked owl pairs in three study areas within the UGM RU (Table 1). Annual activity centers for owl pairs generally were less than half the size of home ranges, suggesting considerable concentration of activity in particular areas. Variation in activity-center size was pronounced across study areas, similar to home-range. The proportion of the home range contained in the activity center was less variable among study areas, ranging from approximately 35 to 41% (Table 1).

This pattern also held in a comparison of seasonal activity centers of individual owls within a single study area (Table 2). Again, activity centers were less than half as large as home ranges, and, as with home ranges, size of activity centers more than doubled during the non-breeding season. Activity centers generally comprised a smaller proportion of pair home ranges during the breeding season, however. Activity typically centers on the nest stand during this season, even in years when the resident pair does not nest.

Spatial overlap between seasonal activity centers was high. Non-breeding season activity centers contained an average of 91% (± 3.1 [SE]) of breeding-season activity centers (Ganey and Block 2005a: Table 5). Because the non-breeding season activity centers were larger than breeding-season activity centers, the proportion of non-breeding season activity centers contained within breeding season activity centers was necessarily lower. The maximum overlap possible here, given the relative size of seasonal activity centers, was 42.6% (± 13.0), and observed overlap was 35.5% (± 9.0 ; Ganey and Block 2005a: Table 5), or 83.3% of maximum potential overlap. Thus, overlap between seasonal activity centers was considerable, indicating that protection of breeding areas provides protection to areas and habitat used throughout the year.

Summary—Space Use

Available information suggests that Mexican spotted owls use relatively large home ranges, with smaller areas of concentrated use embedded within those home ranges. Home-range size appears to vary among geographic areas and/or habitats. Some of that variation may be due to differences in methodology among studies, but we assume that some of the observed variation is real rather than an artifact of methodology. At this time, the relative influences of regional versus local differences in habitat quality on home-range size of Mexican spotted owls remain unclear, although limited information suggests that such local differences can be important (Ganey and others 2005, see also Carey and others 1992, Zabel and others 1995).

Resident owls typically concentrate activity around the nesting area during the breeding season, but they expand their range during the non-breeding season. This concentration of activity during the breeding season occurs even in years

when the resident owls do not nest and may involve territorial defense of the traditional nesting area. Resident owls typically roost in or near the nest stand throughout the breeding season. Ward and Salas (2000: fig. 2) found that >50% of roosts used in the Sacramento Mountains (Basin and Range–East RU) during the breeding season were located <359 m from the nest site used that year. They concluded that roost sites could be used to identify core areas for resident owls where the nest location was unknown, but that this was best done either using roosts where young were observed, or roosts from multiple years in conjunction with information on topography and existing vegetation, especially density of trees >18 in (45 cm) diameter at breast height (dbh).

USDI FWS (1995) formulated conservation guidelines based on data describing space use by Mexican spotted owls. These guidelines recommended maintaining the integrity of breeding-season core areas while limiting management activities in the broader activity center (Protected Activity Center, or PAC) outside of the nest-roost core area.

Habitat Use and Selection

Habitat for a given organism is often defined by vegetative categories like cover types with the understanding that these categories are comprised of multiple resources. Since an organism's habitat can be used for multiple reasons, it is useful to describe habitat requirements according to activity of the organism or the function provided by the habitat. Doing so requires not only a discussion of habitat features associated with a particular activity but also the spatial scale at which that activity occurs (Johnson 1980). In the following sections, we describe Mexican spotted owl habitat according to scale and activity. We use the term habitat to mean the physical elements and biological resources required by the Mexican spotted owl to persist (Hall and others 1997). This includes climatic ranges, types of vegetation, food items, and non-biotic or physical features like topography or geologic structures.

Landscape Scale

Understanding landscape composition of sites occupied by Mexican spotted owls clearly can aid in developing conservation strategies for this species. Three studies in the UGM RU examined landscape composition at various spatial scales around sites occupied by Mexican spotted owls within the UGM RU.

Grubb and others (1997) used air-photo interpretation to compare relative area of four canopy-cover classes (<10, 10–40, 41–70, and >70% canopy cover) between 47 owl nest sites and an equal sample of randomly located sites in the Coconino National Forest, north-central Arizona, at five different spatial scales. They analyzed landscape composition in both circles (radii = 0.06, 0.25, 0.50, 0.75, and 1.0 m [0.1., 0.4, 0.8, 1.2, and 1.6 km]) and concentric “rings,” where outer rings did not include areas sampled in inner rings, and included owl nest sites in landscapes dominated by mixed-conifer forest, pine-oak forest, and rocky canyons containing mixtures of forest types.

Landscape composition (based on concentric rings) differed between owl nest and random sites at all scales, but differences were greatest within 0.5 mi (0.8 km) of nest or roost sites and decreased at increasing spatial scales (Grubb and others 1997: fig. 2). Owl sites contained more area in the >70% canopy-cover class and less area in the <10% canopy-cover class than random sites. The most abundant canopy-cover class on the landscape was 41-70%, except within 0.06 mi (0.1 km) of owl nests, where the >70% canopy-cover class was most abundant.

Peery and others (1999) evaluated the use of specific cover types by Mexican spotted owls in the Tularosa Mountains, New Mexico (GNF study area; see Appendix 2), and the spatial configuration of those cover types. They compared landscape characteristics between 40 owl nest or roost sites and an equal sample of randomly located sites, based on a vegetation map derived from Landsat Thematic Mapper imagery. They evaluated landscape composition at eight spatial scales, in circles with radii ranging from 0.3 mi (0.5 km) to 2.5 mi (4 km; area = 194.9 to 12,424 ac [78.9 to 5,030 ha]). These circles were not spatially independent, because much of the area included in larger circles also was included within smaller circles. For example, 76.5% of their outermost circle consisted of area sampled in the next smaller circle.

In this study, areas around Mexican spotted owl nest and roost sites contained greater amounts of both mature mixed-conifer forest and mature ponderosa pine forest than random sites. Differences between owl and random sites persisted across all spatial scales but were most pronounced within 500 m of the nest or roost and declined with increasing spatial scale. Visual inspection of Figures 1 and 2 in Peery and others (1999) suggests that much of the difference in vegetation composition at larger scales was driven by differences at smaller scales (in other words, to inclusion in larger circles of area sampled by smaller circles). After controlling for the area in various vegetation types, they found no differences between owl and random sites with respect to five indices of spatial configuration of cover types (mean patch size, edge distance, mean nearest-neighbor distance, mean patch shape index, and habitat heterogeneity).

May and Gutiérrez (2002) conducted a similar analysis for owls in an area dominated by ponderosa pine–Gambel oak forest (CNF study area; Appendix 2). They compared 51 owl nest or roost sites with an equal sample of random sites at three spatial scales: a circular plot of 0.5-mi (0.8 km) radius (area = 497 ac [201 ha]), and two 0.25-mi (0.4-km) wide “ring” plots between 0.5 and 1.0 mi (800 and 1600 m) from each nest or roost tree. These scales thus were spatially independent in the sense that outer analysis areas did not include area sampled by inner analysis areas.

Landscape composition in this study area differed between owl and random sites only within the 497 ac (201 ha) analysis area. At this scale, areas around owl nest and roost sites contained more mature mixed-conifer forest than expected based on availability of forest types, as well as more young mixed-conifer forest with canopy cover >55%. Young forests were used by nesting and roosting owls only where residual large (≥ 18 in [45.7 cm] dbh) trees were present (May and Gutiérrez 2002:461). Again, no differences were noted between owl and random sites in three indices of landscape configuration (mean patch size, mean patch shape index, and contagion).

Use of Cover Types and Canopy-Cover Classes Within the Home Range

Home ranges of Mexican spotted owls typically include a diverse array of biotic communities. Throughout their geographic range, they can be found in heavily forested areas as well as in rocky canyons with sparse or no forest cover (Ganey and Dick 1995, Ward and others 1995). Although these forest and canyon environments appear very different in terms of habitat conditions, they represent end points on a gradient of habitat conditions rather than discrete environments used by Mexican spotted owls (Ganey and Balda 1989a). That is, these owls occur along a gradient ranging from areas that are extensively forested and largely lack significant rock outcrops or cliffs, to steep rocky canyons that lack significant forest cover (fig. 8; Rinkevich and Gutiérrez 1996, Willey and van Riper 1998, Willey and Ward 2004).

Understanding how owls use cover types and other habitat features also provides valuable information for resource managers. Information on use of cover types (and other habitat features) by Mexican spotted owls in the UGM RU generally derives from three types of studies. The first study type is observational. These studies provide data on habitat features used, but no information on relative availability of these habitat features to owls. The other two study types differ in methods, but both provide information on use of habitat features relative to availability of those features, and thus allow inference about features selected for or avoided by owls. One study type accomplished this by comparing features at sites used by owls with randomly selected sites within a defined study area. In the UGM RU, this type of study has been conducted in two mark-recapture study areas (CNF, GNF; Appendix 2). These studies involve uniquely marking territorial owls using color bands. Individual owls can then be identified, and their territories delineated, through subsequent resightings of these banded owls. The other approach compares use of habitat features by radio-marked owls with availability of those features within a home range defined based on the movements of those owls. Studies of this type have been conducted within five study areas within the UGM (Appendix 2).

Both types of studies provide valuable information. Studies of radio-marked owls can provide detailed information on habitat use/selection. These studies also can provide information on habitat use of foraging owls as well as on roosting and nesting habitat use, and some have evaluated seasonal differences in use patterns. These studies typically involve relatively few owls, and the generality of the patterns observed therefore, is open to question. In contrast, the mark-recapture studies typically sample larger numbers of owls, allowing for greater inference to the larger population of owls, but are not able to provide information on foraging owls or habitat use during the non-breeding season.

In an example of an observational study, Ganey and Dick (1995: Table 4.1) summarized data by RU on cover types of owl roost and nest sites located by agency surveys from 1989 to 1993. Within the UGM RU, most locations were in mixed-conifer forests (Table 3). Owls also roosted and nested in pine-oak, ponderosa pine, and riparian cover types, in that order of frequency.



Figure 8. Examples of areas occupied along a gradient ranging from extensively forested (top) to rock-dominated (bottom). Bottom photo by D. W. Willey.

Table 3. Percent of Mexican spotted owl nest and roost sites in various cover types within the Upper Gila Mountains and Basin and Range–West Recovery Units. Based on USFS inventory and monitoring data collected from 1990 to 1993 (Ganey and Dick 1995: table 4.1). Cover types follow Vegetation Series in Brown and others (1980). *N* = number of nest or roost sites.

Site type	<i>N</i>	Cover type					
		Evergreen oak	Mixed-conifer	Pine-oak ¹	Ponderosa pine	Riparian ²	Other ³
Upper Gila Mountains Recovery Unit							
Nest	185	0.0	88.6	3.2	1.6	0.5	5.9
Roost	653	0.0	86.7	5.2	1.5	0.5	6.1
Basin and Range–West Recovery Unit							
Nest	74	0.0	68.9	28.4	0.0	2.7	0.0
Roost	165	5.5	49.1	35.8	1.2	4.8	3.6

¹ Primarily ponderosa pine–Gambel oak in the UGM RU; both ponderosa pine–Gambel oak and Madrean pine–oak types occur in the Basin and Range–West RU.

² Includes all broadleaf-deciduous riparian types.

³ Includes spruce-fir forest, Arizona cypress forest, pinyon-juniper woodland, and sites where cover type was recorded as unknown.

The southern portions of the Apache-Sitgreaves and Tonto National Forests occur in the Basin and Range–West RU, an area which differs from the UGM RU in terms of both geology and vegetation types present. A comprehensive discussion of this RU is beyond the scope of this report, but note that habitat use by owls becomes more variable in this RU (Table 3). Specifically, owls in the Basin and Range–West RU occur in vegetation types that are rare or nonexistent in the UGM RU, including evergreen oak woodlands, Madrean pine-oak forests (as opposed to the ponderosa pine–Gambel oak forests used in the UGM RU), and Arizona cypress forests (Ganey and Balda 1989a: Figure 2). Thus, when 4FRI treatments expand to this region, planners will need to recognize these regional differences in habitat use.

Two studies in the UGM RU used the second approach described above, by comparing cover type of owl roost and nest sites with randomly available sites in defined study areas. In the GNF study area, owls selected both roost and nest sites in mixed-conifer forests containing an oak component more frequently than expected by chance (Seamans and Gutiérrez 1995: Figure 1). Mixed-conifer forests lacking an oak component were used next frequently by owls, with very low use of pine/oak forest and woodland cover types (Seamans and Gutiérrez 1995: Figure 1). In the CNF study area dominated by pine-oak forest (78% of total area; May and others 2004: 1055), owls also used mixed-conifer forests more than expected by chance (May and Gutiérrez 2002: Figure 1).

Three studies evaluated use of cover types by radio-marked Mexican spotted owls within the UGM RU. Ganey and Balda (1994) evaluated habitat selection of radio-marked owls in three study areas in Arizona (SFP, WC, and WM; Appendix 2). Patterns of habitat selection differed somewhat both within and among study areas, but some generalities were apparent. All owls roosted primarily in unlogged mixed-conifer forest, with some use of unlogged ponderosa pine forest and very little use of other forest types by roosting owls. Owls foraged in a wider variety of cover types. In general, owls foraged more than or as expected in unlogged forests, based

on the relative availability of those forests. They foraged as expected or less than expected in logged forest types, and rarely foraged in non-forested cover types.

Forest types in this study were classified as “logged” or “unlogged” based on physical evidence (or lack thereof) of tree harvest, such as stumps. Thus, logged areas included a range of treatments. This study, and the other radio-telemetry studies discussed here, also did not evaluate use of forest edges for foraging, due to the spatially imprecise nature of the underlying location data for radio-marked owls (for example, Ganey and others 1999, 2003). Finally, most unlogged forests within the Walnut Canyon (WC) study area occurred on steep canyon slopes. These forests were interspersed with rocky outcrops and cliffs, and owls used these outcrops and cliffs, as well as the interspersed forests, for both foraging and roosting (fig. 9).

Stacey and Hodgson (1999) studied radio-marked Mexican spotted owls in the San Mateo Mountains, New Mexico. Owls in this study roosted exclusively in mixed-conifer or mixed-conifer/oak forest; no roosts were located in ponderosa pine forest or pinyon–juniper woodland, although those types were common in the study area (Stacey and Hodgson 1999: fig. 1).

The above study areas all contained considerable expanses of mixed-conifer forest. Ganey and others (1999) evaluated use of three cover types (ponderosa pine forest, ponderosa pine–Gambel oak forest, and meadow) and four canopy-cover classes (<20, 20-39, 40-59, and >60% canopy cover), as well as seasonal habitat use of radio-marked owls, in a study area dominated by pine-oak forest (BMC; Appendix 2). Home ranges were dominated by pine-oak forest in both the breeding (mean = 60.9% of home-range area) and non-breeding season (mean = 60.1%). On average, meadows comprised 2.4 and 2.6% of breeding and non-breeding seasons ranges, respectively (Ganey and others 1999: Table 2), with the remainder comprised of ponderosa pine forest. Owls foraged (>61% of locations in both seasons) and especially roosted (72 and 64% of locations in the breeding and non-breeding seasons, respectively) primarily in pine-oak forest during both seasons. Radio-marked owls rarely used the meadow cover type for either activity in either season (<2.2% of foraging locations and <0.5% of roosting locations in both seasons; Ganey and others 1999: Table 2). Cover types in this study were classified using plot data linked to USFS stand maps. Therefore, meadows as used here refers to relatively large (≥ 10 ac [4 ha]) openings, rather than to smaller openings within forest stands.

In contrast to cover types, relative area of canopy-cover classes differed significantly between seasonal ranges. Breeding season ranges contained significantly greater proportions of area with $\geq 60\%$ canopy cover (19.9 vs. 8.4%) and less area with 20-39% canopy cover than non-breeding season ranges (34.1 vs. 43.0%; Ganey and others 1999: Table 3). Relative use of canopy-cover classes varied between seasons but differed from availability in both seasons. Owls foraged and roosted more than expected in areas with canopy cover >60% in both seasons. Use of this canopy-cover class was particularly pronounced for roosting during the breeding season (85% of locations; Ganey and others 1999: Table 3). No other canopy-cover classes were used more than expected in either season.



Figure 9. Mexican spotted owl roosting on a cliff ledge (upper left). Also note two juvenile owls in a nest on a cliff ledge (center). Although roosting and nesting on cliffs is less common in the Upper Gila Mountains Recovery Unit than in other areas such as the Colorado Plateau, it does occur. The radio-marked pair of resident owls from this territory moved regularly between cliff and tree roosts, and in different years they nested both on this cliff ledge and in trees.

Habitat Characteristics of Areas Used by Owls

As discussed above, different study designs (mark-recapture vs. radio-telemetry) have been used in studies that characterized areas used by owls. In addition, studies sampled habitat characteristics at different spatial scales, and scale differences also can influence the results of analyses of habitat use. Consequently, we will discuss characteristics of habitats used for different activities by spatial scale. We recognize three activities here (nesting, roosting, and foraging) and three spatial scales (stand, site, and tree). Stand refers to USFS-designated forest stands, which are delineated to identify discrete areas of relatively homogeneous vegetation, with a typical minimum size of approximately 10 ac (4 ha). Habitat characteristics within stands are estimated based on multiple sample plots within the stand. Site refers to a small area sampled around a nest, roost, foraging, or random site using a single sampling plot, and tree refers to features of roost and nest trees sampled within those single plots. The stand scale may be more relevant to many forest management applications, but much of the information available on Mexican spotted owls derives from data gathered at the scale of sites or trees.

Sampling methods and parameters sampled also differed among studies. Some studies used variable-radius plots while others used fixed-radius plots. And some studies sampled canopy closure whereas others sampled canopy cover. Canopy closure measures “the proportion of the sky hemisphere obscured by vegetation when viewed from a single point,” whereas canopy cover measures “the area of the ground covered by a vertical projection of the canopy” (Jennings and others 1999). In the studies discussed here, canopy closure was estimated using a spherical densiometer, and canopy cover was sampled using a sighting tube. These differences in sampling methods and parameters sampled hinder direct comparisons even between studies that sampled at the same scale.

Stand Scale—All of our information on habitat use at the stand scale derives from studies of radio-marked owls. Ganey and others (1999) compared characteristics of stands used by owls with those of stands within the home range that lacked documented use by owls in a study area dominated by ponderosa pine–Gambel oak forest (BMC; Appendix 2). Stands used by foraging owls ($n = 190$ stands) did not differ between seasons, so foraging stands were pooled across seasons for comparisons. Stands used by foraging owls had significantly greater canopy cover ($42.9 \pm 1.2\%$ [SE] vs. $38.8 \pm 1.3\%$) than stands within the home range lacking documented use by radio-marked owls ($n = 138$; Ganey and others 1999: Table 4).

Characteristics of stands used by roosting owls differed between seasons, so comparisons between used and unused stands were stratified by season. Stands used for roosting differed from unused stands in both seasons. The primary difference involved canopy cover, which was significantly greater in stands used for roosting than in unused stands in both seasons (Table 4). Stands used by owls also had significantly greater live tree basal area and Gambel oak basal area

Table 4. Selected characteristics of stands within the home range used and not used for roosting by radio-marked Mexican spotted owls during the breeding and non-breeding seasons in a study area (Bar-M Canyon; Appendix 2) dominated by ponderosa pine–Gambel oak forest, Upper Gila Mountains Recovery Unit, Arizona. Shown are means and standard errors (SE); numbers of stands shown in parentheses. From Ganey and others (1999: Table 5)

Parameter	Breeding season ¹				Non-breeding season ¹			
	Used (34)		Unused (119)		Used (138)		Unused (190)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Live tree basal area (ft ² ac ⁻¹) ²	122.8	1.3	105.0	3.9	109.8	2.2	101.9	2.2
Oak basal area (ft ² ac ⁻¹) ²	20.5	3.5	11.3	2.6	15.2	0.9	10.9	0.4
% oak basal area ³	16.7		10.8		13.8		10.7	
Canopy cover (%)	53.2	3.1	39.4	1.2	44.1	1.2	38.7	1.4

¹ Seasons: Breeding = 1 Mar–30 Aug ($n = 8$ owls), Non-breeding = 1 Sep–28 Feb ($n = 14$ owls).

² To convert basal areas to m² ha⁻¹, divide by 4.3554.

³ Percent of live tree basal area contributed by Gambel oak, calculated from table values as: (Oak basal area / Live tree basal area) * 100.

than unused stands, and Gambel oak comprised a greater proportion of overall basal area in used than in unused stands. All oaks sampled in this study were >4 in (10 cm) in dbh, 90% were >6 in (16 cm) dbh, 75% were >9 in (23 cm) dbh, and 50% were >13 in (33.5 cm) dbh; based on further analysis of tree data summarized by Ganey and others 1999). Thus, these basal areas primarily relate to tree-form Gambel oak, rather than to clumps of Gambel oak in shrub form.

Ganey and others (1999) also compared stands used for foraging with stands used for roosting. Stands used by foraging owls differed from stands used for roosting during the breeding season, but not during the non-breeding season. Stands used for roosting during the breeding season had significantly greater canopy cover ($53.2 \pm 3.1\%$ vs. $42.9 \pm 1.2\%$) and density of live trees (195.2 ± 18.3 vs. 182.7 ± 10.9 trees ac⁻¹ [482.2 ± 45.2 vs. 451.2 ± 27.0 trees ha⁻¹]) than stands used for foraging.

Ganey and others (2003) used this same data set to further evaluate characteristics of stands used by owls. Specifically, they summarized median tendencies and variability in stands used by owls, to better characterize the range of conditions typical in stands used. In general, stands used for roosting were less variable than stands used for foraging ($n = 150$ stands). All stands used for roosting were also used for foraging, whereas owls did not roost in all stands used for foraging. In addition, roost stands used during the breeding season ($n = 31$) were less variable than roost stands used during the non-breeding season ($n = 116$). Owls were never observed roosting in stands with basal area <60 ft² ac⁻¹ (13.8 m² ha⁻¹) during the breeding season (fig. 10, top), or in stands with oak basal area < 23 ft² ac⁻¹ (5.3 m² ha⁻¹) (fig. 10, middle), suggesting some potential thresholds for use in managing habitat for Mexican spotted owls in areas dominated by pine-oak forest. As noted above, basal area cited here refers to tree-form rather than shrub-form Gambel oak. They also did not roost in stands with canopy cover <25% during the breeding season, and 75% of stands used for roosting during this season had canopy cover >40% (fig. 10, bottom), suggesting some additional management thresholds.

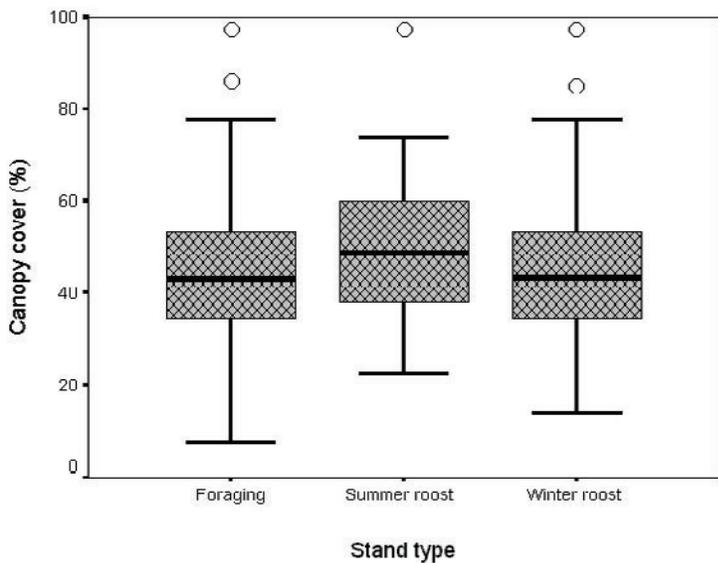
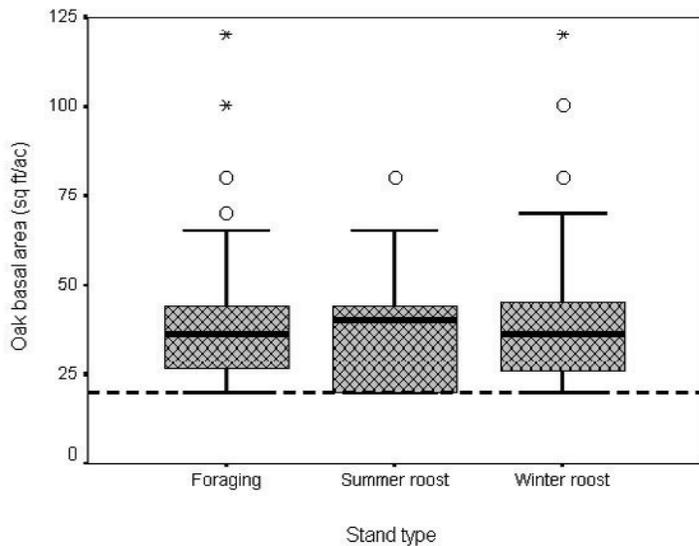
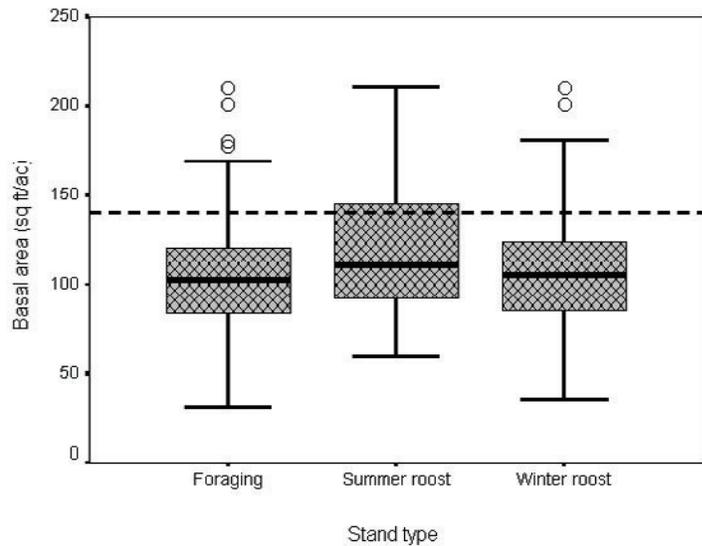


Figure 10. Selected characteristics of stands used for foraging and roosting by radio-marked Mexican spotted owls in pine-oak forest, Upper Gila Mountains Recovery Unit. Based on 150 stands used by foraging owls, and 31 and 166 stands used by roosting owls during the breeding and non-breeding season, respectively. The box denotes the interquartile range (25th to 75th percentile), the black line within the box denotes the median (50th percentile), and the whiskers indicate the range in the data excluding outliers (circles, defined as observations >1.5 box lengths outside the box). Top: Basal area of live trees. The dotted line indicates the recovery plan (USDI FWS 1995) recommendation for tree basal area in pine-oak forest (139 ft² ac⁻¹ [32 m² ha⁻¹]); almost 75% of roost stands used during the breeding season fell below this recommendation. Owls did not roost in stands with basal area <60 ft² ac⁻¹ (13.8 m² ha⁻¹) during the breeding season, and 75% of stands used for roosting during this season had basal area >90 ft² ac⁻¹ (20.7 m² ha⁻¹). Middle: Basal area contributed by Gambel oak. The dotted line indicates the recovery plan (USDI FWS 1995) recommendation for oak basal area in pine-oak forest (20 ft² ac⁻¹ [4.6 m² ha⁻¹]); all stands used by owls fell above this recommendation. Owls did not roost in stands with oak basal area <23 ft² ac⁻¹ (5.3 m² ha⁻¹) during the breeding season, and 50% of stands used for roosting during this season had oak basal area >35 ft² ac⁻¹ (8.0 m² ha⁻¹). Bottom: Canopy cover (%). Owls did not roost in stands with canopy cover <25% during the breeding season, and 75% of stands used for roosting during this season had canopy cover >40%. Reprinted from Ganey and others (2003: Figure 2). Used by permission from the Society of American Foresters.

Similar information does not exist for mixed-conifer stands in the UGM RU. However, Ganey and others (2003) provided a similar analysis for a study area dominated by mesic mixed-conifer forest in the Basin and Range-East RU. We do not know how similar patterns of habitat use are between these RUs, but we present these data in the absence of data specific to the UGM RU.

In this study area, stands used for both roosting and foraging were pooled across seasons. As in the pine-oak study area, stands used for roosting generally were less variable than stands used for foraging, and all stands used for roosting were used for foraging, whereas the converse was not true. Only one stand used by roosting owls during the breeding season had basal area $<75 \text{ ft}^2 \text{ ac}^{-1}$ ($17.2 \text{ m}^2 \text{ ha}^{-1}$) (fig. 11, top), suggesting a potential threshold for use in managing habitat for Mexican spotted owls in areas dominated by mesic mixed-conifer forest. All but two stands used for roosting had canopy cover $>40\%$, and 75% of roost stands had canopy cover $>60\%$ (fig. 11, bottom), suggesting some additional management thresholds.

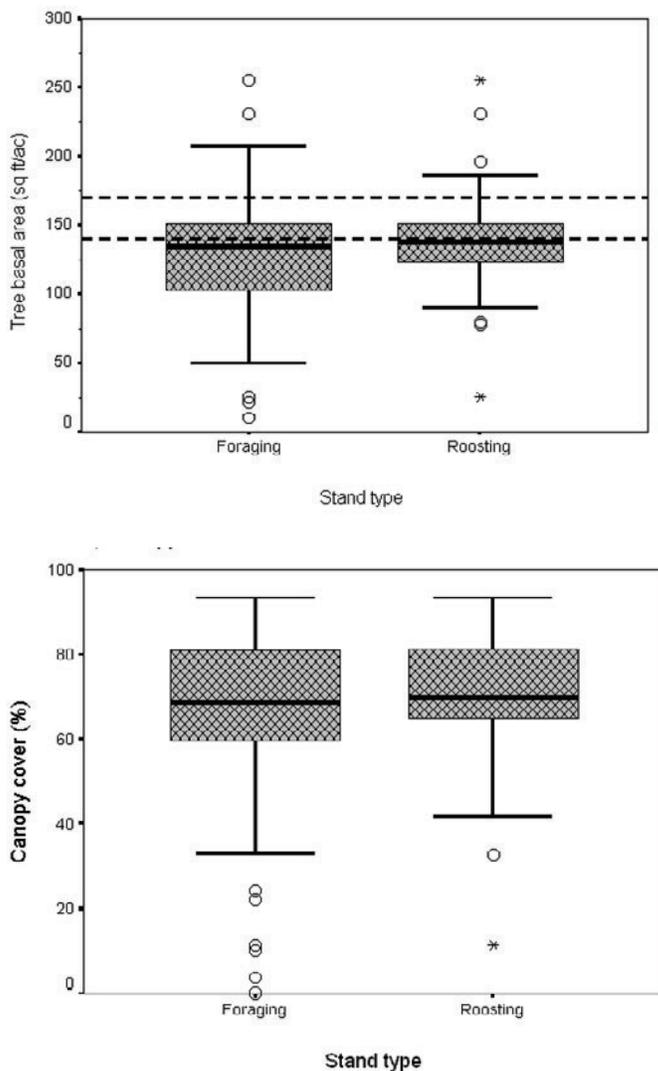


Figure 11. Selected characteristics of stands used for foraging and roosting by radio-marked Mexican spotted owls in a study area dominated by mixed-conifer forest, Sacramento Mountains, Basin and Range-East Recovery Unit. Based on 94 and 43 stands used by foraging and roosting owls, respectively. The box denotes the interquartile range (25th to 75th percentile), the black line within the box denotes the median (50th percentile), and the whiskers indicate the range in the data excluding outliers (circles, defined as observations >1.5 box lengths outside the box). Top: Basal area of live trees. The dotted lines indicate recommendations for basal area in USDI FWS (1995). These recommendations called for retaining basal area at or above the lower value ($139 \text{ ft}^2 \text{ ac}^{-1}$ [$32 \text{ m}^2 \text{ ha}^{-1}$]) on 20% of the landscape, and at or above the upper value ($170 \text{ ft}^2 \text{ ac}^{-1}$ [$39 \text{ m}^2 \text{ ha}^{-1}$]) in half of that 20% of the landscape (i.e., 10% of the landscape). The lower recommendation approximates the median value of basal area in stands used by roosting owls. Owls did not roost in stands with basal area $<60 \text{ ft}^2 \text{ ac}^{-1}$ ($13.8 \text{ m}^2 \text{ ha}^{-1}$) during the breeding season, and 75% of stands used for roosting during this season had basal area $>90 \text{ ft}^2 \text{ ac}^{-1}$ ($20.7 \text{ m}^2 \text{ ha}^{-1}$). Bottom: Canopy cover. All but two stands used for roosting had canopy cover $>40\%$, and 75% of stands used for roosting had canopy cover $>60\%$. Reprinted from Ganey and others (2003: Figure 3). Used by permission from the Society of American Foresters.

Site Scale—A number of studies provided information on habitat characteristics of sites used by Mexican spotted owls in the UGM RU. As noted above, information derives from two types of studies, mark-recapture and radio-telemetry, and we will discuss studies in that order.

Seamans and Gutiérrez (1995) compared habitat characteristics between 27 owl nest sites and an equal number of randomly located sites in the GNF study area using variable-radius plots. Nest-site plots were centered on the nest tree, and random plots were centered on a randomly selected tree ≥ 10.7 in (27.3 cm) dbh, the minimum diameter among the 27 nest trees. This was an attempt to minimize the potential bias caused by centering nest-site plots on a large tree and random plots on trees of any size. Most nests (96%) were located on the lower two-thirds of slopes, and the mean slope aspect was northerly and differed significantly from random plots. Nest plots had significantly greater tree basal area, basal area of mature trees, and canopy closure than random plots, and mature trees contributed a greater proportion of overall basal area in nest than in random plots (Table 5).

Seamans and Gutiérrez (1995) also compared characteristics between 78 owl roost sites and 71 random sites within this study area. Most roosts (97%) were located on the lower two-thirds of slopes, and the mean slope aspect was northerly but did not differ significantly from random plots. Roost plots had significantly greater tree basal area, basal area of mature trees, and canopy closure than random plots (Table 5). Mature trees contributed a greater proportion of overall basal area in roost than in random sites, but the difference was not as great as that observed between nest and random sites (Table 5).

May and others (2004) conducted similar analyses in a study area in Arizona (CNF) dominated by ponderosa pine–Gambel oak forest. They compared nest sites both to random sites located throughout the study area ($n = 41$ for each site type), and to random sites located within the same stand as the nest site ($n = 34$ matched plots for site types in the latter analysis; all plots were variable radius).

Table 5. Selected characteristics (mean and standard deviation) of Mexican spotted owl nest and roost sites and randomly located sites in the Tularosa Mountains, Gila National Forest, New Mexico (GNF study area). From Seamans and Gutiérrez (1995: Tables 1 and 2). Characteristics sampled in variable radius plots, with separate sets of random plots used in comparisons of nest and roost sites, respectively. Plot sample sizes shown in parentheses. Most nests and roosts (>95%) were in mixed-conifer forest (Seamans and Gutiérrez 1995: Figure 1).

Parameter	Nest sites (27)		Random sites (27)		Roost sites (78)		Random sites (71)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Live tree basal area (ft ² ac ⁻¹) ¹	110.2	57.5	82.3	47.0	138.1	61.8	86.2	51.4
Mature tree ² basal area (ft ² ha ⁻¹) ¹	54.0	45.7	18.7	26.1	39.2	34.4	16.1	24.4
% mature basal area ³	49.0		22.7		28.4		18.7	
Canopy closure (%)	75.9	14.1	56.3	20.4	85.2	9.9	50.5	22.4

¹ To convert basal areas to m² ha⁻¹, divide by 4.3554.

² Trees ≥ 18 in (45.8 cm) dbh.

³ Calculated from table values as: (Mature tree basal area/Live tree basal area) * 100.

Slope aspect at nest sites was fairly variable, with a mean tendency toward placement on slopes with north or northwest aspects. Eighty percent of nests were located on the lower two-thirds of slopes. Owl nest sites in this area had significantly greater canopy closure, percent slope, and mature/old growth hardwood basal area than did random plots from throughout the study area (Table 6; note that this table summarizes data for more plots than were used in analyses, based on values in May and others 2004: Table 3). Although hardwood species were not specified, Gambel oak is the most common hardwood within this study area and presumably contributed the bulk of hardwood basal area. Fewer significant differences were observed between nest sites and random sites located within the nest stand, but nest sites occurred on steeper slopes and contained greater mature/old growth hardwood basal area than nest-stand sites.

May and others (2004) also compared characteristics of roost sites and random sites located throughout the study area ($n = 75$ for both site types). Similar to nest sites, roost sites had greater canopy closure, percent slope, and mature/old growth basal area than did random sites from throughout the study area (Table 6). They also compared characteristics between 27 matched pairs of nest and roost sites. Nest sites had significantly greater mature/old growth hardwood basal area than roost sites (Table 6).

Ganey and Balda (1994) compared habitat characteristics among owl foraging, roosting, and randomly located sites within home ranges of six radio-marked owls representing four owl territories in two study areas in Arizona (SFP and WM, Appendix 2; WC was omitted due to the difficulty involved in sampling plots on the steep, rocky slopes used by owls in that area). Because sampled plots were small (0.1-ac [0.04-ha] circles), and because individual foraging locations based on radio-telemetry were imprecise, foraging plots were randomly located within high-use foraging areas defined by concentrations of foraging locations.

Table 6. Selected characteristics (mean and standard deviation) for Mexican spotted owl nest and roost sites and two kinds of randomly located sites in the CNF study area (Coconino National Forest), Upper Gila Mountains Recovery. From May and others (2004: Table 3). Characteristics sampled within variable radius plots. Although this study area was dominated by ponderosa pine and ponderosa pine–Gambel oak forest (see Table 1), 38.1% of nests and 44.6% of roosts were located in mixed-conifer forest.

Parameter	Plot type ¹							
	Owl				Random			
	Nest sites		Roost sites		Stand		Study area	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mature/OG BA (ft ² ac ⁻¹) ²	54.0	49.2	32.7	37.5	27.4	33.5	14.8	24.8
Mature/OG hardwood BA (ft ² ac ⁻¹) ³	14.4	22.7	5.2	12.6	3.1	8.3	2.2	6.5
Total hardwood BA (ft ² ac ⁻¹)	45.7	53.1	37.1	60.1	29.6	40.1	14.4	28.3
Slope (%)	27.6	14.3	27.0	14.8	20.9	12.5	8.7	7.9
Canopy closure (%)	79.0	11.1	83.8	14.8	73.8	18.1	50.0	21.4

¹ Sample sizes: 97 nest sites, 176 roost sites, 80 random plots within nest stands, 110 random plots within the larger study area.

² Trees ≥ 18 in (45.7 cm) dbh. To convert basal areas to m² ha⁻¹, divide by 4.3554.

³ Hardwood trees ≥ 18 in (45.7 cm) dbh.

Tree and snag densities and basal areas, canopy closure, and log numbers all were greatest at roost sites, intermediate in owl foraging areas, and lowest at randomly available sites (Ganey and Balda 1994: Table 4).

Stacey and Hodgson (1999) compared roost sites of radio-marked owls ($n = 6$ adult and 3 juvenile owls from three territories) and random sites in the San Mateo Mountains, based on 0.1-ac (0.04-ha) circular plots. Most roost sites in this area were located in drainage bottoms or on the lower third of slopes. Because roosts occurred only in mixed-conifer forest in this study area, they compared roost sites ($n = 64$) separately to random sites in all cover types ($n = 69$) and to random sites that occurred in mixed-conifer forest ($n = 36$). Mean canopy closure was significantly greater at roost sites than at random sites when all random sites were used, but it did not differ significantly when only random sites in mixed-conifer forest were used (Table 7). Roost plots had significantly greater basal area of Douglas-fir, Gambel oak, and southwestern white pine than all random sites, and lower basal area of ponderosa pine and pinyon and juniper (Stacey and Hodgson 1999: Table 1). However, only Gambel oak basal area remained significantly greater when the comparison was restricted to random sites within mixed-conifer forest, and the proportion of overall tree basal area contributed by Gambel oak was approximately four times greater in roost sites than in either set of random sites (Table 7). Roost sites also had lower density of medium-sized conifers (15-30 cm dbh) and greater density of small deciduous trees than either set of random sites (Stacey and Hodgson 1999). Thus, owls in this area roosted in structurally complex mixed-conifer sites with a prominent oak component.

Ganey and others (2000) described characteristics of roost sites used by radio-marked owls during the breeding ($n = 146$ roost sites) and non-breeding ($n = 262$) seasons in ponderosa pine–Gambel oak forest (BMC study area). Many characteristics of roost sites were similar between seasons, but canopy cover was greater at roost sites used during the breeding season ($74 \pm 17\%$ [*SD*]) than at those used during the non-breeding season ($59 \pm 18\%$; Ganey and others 2000: Table 2).

Table 7. Selected habitat characteristics (mean and standard deviation) of roost sites used by radio-marked Mexican spotted owls in the San Mateo Mountains, Cibola National Forest, New Mexico, and two types of random plots. $N = 64$ roost plots, 69 random plots in all forest types, and 36 random plots in mixed-conifer forest. Source: Stacey and Hodgson (1999). Characteristics sampled in 0.1-ac (0.04-ha) circular plots. All roosts were in mixed-conifer forest (Stacey and Hodgson 1999: Figure 1)

Parameter	Random plots					
	Roost plots		All forest types		Mixed-conifer forest	
	Mean	SD	Mean	SD	Mean	SD
Canopy closure (%)	59.2	17.2	42.6	20.1	51.9	18.7
Tree basal area (ft ² ac ⁻¹) ¹	85.8	42.7	73.6	37.5	84.5	38.8
Gambel oak basal area (ft ² ac ⁻¹) ¹	24.0	20.5	4.8	8.7	6.1	10.5
% Gambel oak basal area ²	27.9		6.5		7.2	

¹ To convert basal area to m² ha⁻¹, divide by 4.3554.

² Calculated from above table values as: (Gambel oak basal area/ Tree basal area) * 100.

Owls roosted primarily in pine-oak forest in both seasons (99.3 and 96.9 of roost sites in the breeding and non-breeding season, respectively). Mean roost aspect shifted from northwest during the breeding season to southwest during the non-breeding season (Ganey and others 2000: Table 4), and roosts were not highly concentrated on any portion of slopes during either season (Ganey and others 2000: Table 3).

Tree Scale—Information describing roost and nest trees generally derives from the same studies mentioned above. Seamans and Gutiérrez (1995) compared characteristics of 27 nest trees located in the GNF study area with 27 randomly located trees within a 150-m radius of nest trees. Nest trees were significantly larger in diameter, taller, and older than randomly located trees within the vicinity (Table 8). Most nests were in Douglas-fir trees in this study area (Table 9) and most were in dwarf mistletoe brooms (Table 10; fig. 12).

May and others (2004) sampled 114 nest trees in the CNF study area. Sixty-two percent of nest trees were located in pine-oak forest, which comprised 78% of the study area, and 38% of nests were located in mixed-conifer forest, although mixed-conifer forest comprised only 5% of the study area (May and others 2004: 1055). Owls nested primarily in Gambel oak and ponderosa pine trees, although they also used Douglas-fir, white fir, quaking aspen, and Engelmann spruce (Table 9), and 76% of all nests were in trees >18 in (45.7 cm) dbh. Most nests were located in cavities accessed through a hole in the side of the bole (fig. 13), platforms in trees, or cavities in broken-topped trees (Table 10, fig. 14). Most nests in side cavities were in Gambel oak trees, and most platform nests were in ponderosa pine trees.

Fifty-five percent of 210 roost trees sampled in the CNF were located in pine-oak forests, with 45% in mixed-conifer forest (May and others 2004). Owls roosted primarily in ponderosa pine, Gambel oak, and white fir trees (Table 9). Owls roosted in medium-sized trees, with 76% of roosts located in trees <18 in (45.7 cm) dbh.

Table 8. Selected characteristics of 27 Mexican spotted owl nest trees and 27 randomly located trees within the nest stand in the Tularosa Mountains, Gila National Forest, New Mexico (GNF study area). From Seamans and Gutiérrez (1995: Table 3). Most nests (>95%) were in mixed-conifer forest (Seamans and Gutiérrez 1995: Figure 1).

Parameter	Nest trees		Random trees	
	Mean	SD ¹	Mean	SD ¹
Age (yrs)	163.6	44.8	119.6	64.6
Tree height (ft) ²	89.2	21.3	59.7	28.2
Dbh (in) ³	23.9	8.8	17.0	10.0

¹ Standard deviation

² To convert height to m, divide by 3.28.

³ Diameter at breast height. To convert to cm, multiply by 2.54.

Stacey and Hodgson (1999) described roost trees used by radio-marked owls in the San Mateo Mountains, New Mexico. Owls there roosted mainly in Douglas-fir, Gambel oak, and southwestern white pine trees (Table 9). Again, many roost trees were medium in size (mean dbh = 12.2 ± 5.6 in [*SD*; 31 ± 14.3cm]).

Table 9. Tree species use (%) by nesting or roosting Mexican spotted owls in various study areas, Upper Gila Mountains Recovery Unit. Most nests in GNF and most nests and roosts in CNF were in mixed-conifer forest. All roosts in SMM were in mixed-conifer forest. Most roosts in BMC were in ponderosa pine–Gambel oak forest, with the remainder in ponderosa pine forest.

Tree species	Study area (and site type [nest or roost] or season [breeding or non-breeding]) ¹					
	GNF	CNF		SMM	BMC	
	Nest	Nest	Roost	Roost	Roost (B) ²	Roost (NB) ²
Douglas-fir	78	12.3	13.8	47	0.0	0.0
White fir	11	8.8	23.3	U ³	0.0	0.0
Ponderosa pine	7	36.8	37.6	U ³	63.5	91.1
Southwestern white pine	4	0.0	0.0	13	0.0	0.0
Gambel oak	0	40.4	24.3	19	36.5	8.9
Quaking aspen	0	0.9	0.0	U ³	0.0	0.0
Engelmann spruce	0	0.9	0.5	U ³	0.0	0.0
New Mexico locust	0	0.0	0.5	U ³	0.0	0.0

¹ Sources and sample sizes: GNF (Tularosa Mountains, Gila National Forest, New Mexico) = Seamans and Gutiérrez 1995; 27 nest trees; CNF (Coconino National Forest, Arizona) = May and others 2004, 114 nest and 210 roost trees; SMM (San Mateo Mountains, Cibola National Forest, New Mexico) = Stacey and Hodgson 1999, 64 roost trees; BMC = Ganey and others 2000, 146 roost trees during the breeding season [B] and 262 roost trees during the non-breeding season [NB]. Study areas described in Appendix 2.

² Season: B= breeding (1 Mar–30 Aug), NB = non-breeding (1 Sep–28 Feb).

³ U = unknown; no data reported on use or non-use of these species.

Table 10. Use of nest structures (%) by Mexican spotted owls in two study areas, Upper Gila Mountains Recovery Unit.

Nest structure	Study area (sample size) ¹	
	GNF (27)	CNF (114)
Dwarf mistletoe broom	61.0	
Squirrel nest	10.5	
Raptor nest	10.5	
Cavity in bole		43.0
Cavity in broken top		12.0
Cavity (type unspecified)	7.0	
Debris platform	7.0	
Platform (type unspecified) ²		44.7
Cliff ledge	4.0	

¹ Sources: GNF (Tularosa Mountains, Gila National Forest, New Mexico) = Seamans and Gutiérrez (1995), >95% of these nests were located in mixed-conifer forest; CNF (Coconino National Forest, Arizona) = May and others (2004), 62% of these nests were located in ponderosa pine–Gambel oak forest and 38% in mixed-conifer forest, but structure use was not described by forest type. Study areas are described in Appendix 2.

² This category may have included other categories such as squirrel nest, raptor nest, and debris platform.



Figure 12. Platform nest used by Mexican spotted owls in a dwarf mistletoe broom. Top photo shows the broom (arrow), bottom photo is a closer view of the platform within the broom. The female's head can be seen (arrow) as she sits in the nest.



Figure 13. Nest cavity used by Mexican spotted owls (adult and juvenile owl shown) in the side of a large Gambel oak tree.



Figure 14. Mexican spotted owl nest cavities in a broken-topped snag (left) and tree (right). The nest cavity entrance in the live tree (approximate location denoted by arrow) is blocked by foliage, but the tree form shown is one commonly used by Mexican spotted owls. This cavity formed where the original tree top broke off. Note how a secondary branch, or bayonet limb (left of nest cavity), has grown up to overtop the cavity. This branch provides shade and cover to the cavity opening.

Ganey and others (2000) described characteristics of roost trees used by radio-marked owls during the breeding and non-breeding seasons in ponderosa pine–Gambel oak forest, Arizona. Use of Gambel oak by roosting owls declined greatly from the breeding to non-breeding season, whereas use of ponderosa pine increased (Table 9). Size of roost trees used was similar between seasons (mean dbh = 12.7 ± 5.6 [*SD*] vs. 12.2 ± 4.6 in [32.3 ± 14.2 vs. 31.1 ± 11.6 cm] during the breeding and non-breeding seasons, respectively).

No similar information is available on roost-tree use during the non-breeding season in mixed-conifer forest within the UGM RU, but Ganey and others (2000) summarized information from two study areas containing mixed-conifer forest in the Sacramento Mountains, New Mexico (Basin and Range–East RU). In general, fewer differences were observed in roost characteristics between seasons in these study areas than in the pine-oak study area (Ganey and others 2000: Tables 2 and 3). As in the pine-oak forest, use of Gambel oak declined from the breeding season (14.7 and 11.6% of roost trees in the two study areas) to the non-breeding season (6.6 and 8.5% of roost trees; Ganey and others 2000: Table 3).

Summary—Habitat Use and Selection

Studies of spotted owl habitat use and selection occurred at different spatial scales, using different study designs and sampling methods and often sampled different parameters. All of these differences make direct comparisons among studies difficult. Despite these differences in methodology, there are striking similarities in observed patterns of habitat use across studies. Thus, available data on habitat use of Mexican spotted owls in the UGM RU strongly suggest several emergent patterns.

Owls in this region occur in both heavily forested areas and in areas featuring combinations of forested slopes and rocky outcrops. Although owls occur in and use several forest cover types, and although pine-oak forest can be locally important, they most commonly occur in mixed-conifer forest (Table 3, see also Seamans and Gutiérrez 1995, Peery and others 1999, Stacey and Hodgson 1999, May and Gutiérrez 2002, and May and others 2004). Mixed-conifer forest appears to be particularly important in terms of nesting and roosting habitat, followed by pine-oak forest (fig. 15).

Owls generally selected home ranges in landscapes containing more mature forest or more young forest with residual large trees than randomly available landscapes (Peery and others 1999, May and Gutiérrez 2002), and/or greater amounts of closed-canopy forest (Grubb and others 1997). Selection for nest or roost sites was most pronounced at relatively small spatial scales (for example, within 0.5 mi [0.8 km] of the nest or roost) and declined at increasing spatial scales (for example, Grubb and others 1997, Peery and others 1999, May and Gutiérrez 2002). In general, the scale at which differences between owl and random sites were most pronounced (497 ac [201 ha]; Grubb and others 1997, May and Gutiérrez 2002) correlated reasonably well with the PAC size (600 ac [243 ha]) recommended in USDI FWS (1995). Indices of landscape pattern evaluated did not differ between owl and



Figure 15. Photos showing mixed-conifer forest (top) and ponderosa pine–Gambel oak (bottom) forest types occupied by Mexican spotted owls. The mixed-conifer photo shows an open canyon bottom surrounded by closed-canopy forest, which may provide owls with both roosting/nesting habitat (interior forest) and foraging habitat along the forest edge in proximity. The pine-oak photo shows several features that may be important to Mexican spotted owls. These include patches of closed canopy forest as well as a relatively lush herbaceous understory that provides food and cover for mammalian prey species. There is a well-developed midstory of Gambel oak, which provides additional shade during the summer as well as canopy layering and a possible food source for prey. Also note the large oak tree (arrow), and the down logs, which may provide dens and additional cover for mammalian prey.



random sites (Peery and others 1999, May and Gutiérrez 2002). These findings collectively suggest that amount of suitable habitat in an area may be more important than the spatial arrangement of such habitat.

At both stand and site scales, habitats used and selected for roosting and nesting appear to be fairly similar in structure and differ significantly from randomly available habitat (for example, Seamans and Gutiérrez 1995, Ganey and others 1999, Stacey

and Hodgson 1999, May and others 2004). Roost and nest sites typically occur in closed-canopy stands with high basal area of live trees. Mature trees typically contribute a high proportion of overall basal area at nest and roost sites (fig. 16), and Gambel oak (and/or other hardwoods) also appears to be an important feature of roost and nest areas within both mixed-conifer and pine-oak forests (fig. 17; Seamans and Gutiérrez 1995, Ganey and others 1999, Stacey and Hodgson 1999, May and others 2004). Large oak trees appear to be particularly important for providing nest sites (fig. 13), whereas both large and smaller hardwoods contribute importantly to habitat structure and complexity and provide additional shade and hiding cover for roosting owls (fig. 17). Tree density was not identified as an important discriminating variable in most study areas. Thus, although owls appear to be selecting for closed-canopy stands with large, mature trees and high basal area, they are not necessarily selecting for dense stands. This is an important point for land managers to consider in evaluating and managing Mexican spotted owl habitat.

Owls appear to be less selective (at both scales) in habitats used for foraging (Ganey and Balda 1994, Ganey and others 1999, 2003). Thus, within areas containing suitable roosting and nesting habitat, owls forage in a broader array of both cover types and structural conditions.

Although information on seasonal habitat use is limited, there is some evidence that resident owls wander more widely during the non-breeding season (see **Home Range**, above) and that owls may use more open habitats during the non-breeding season (Ganey and others 1999, 2000, 2003).

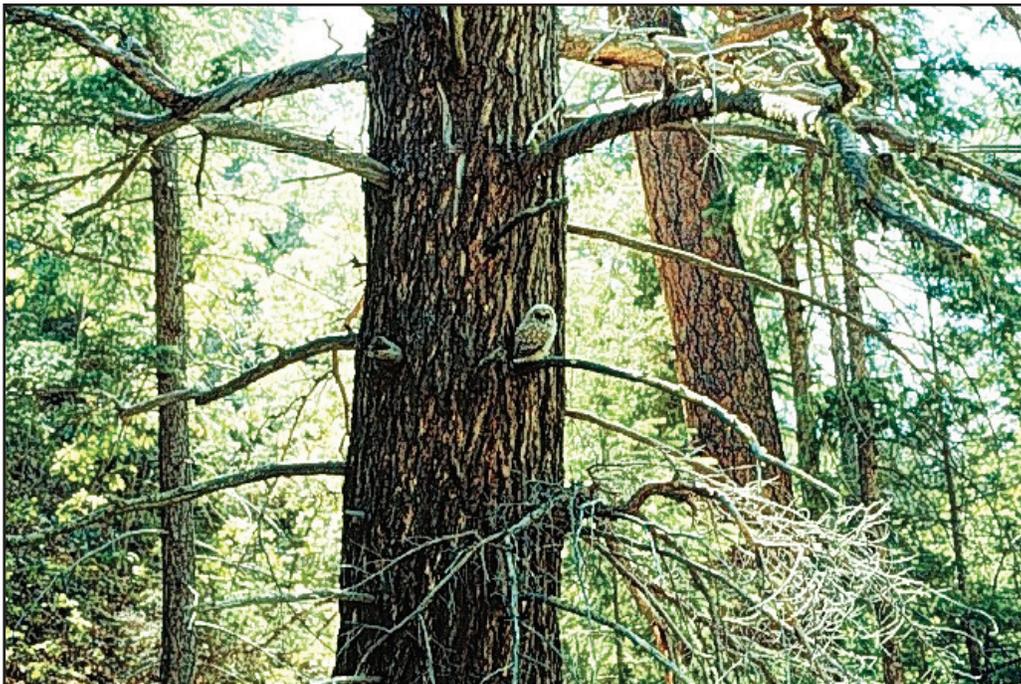


Figure 16. Juvenile Mexican spotted owl perched in a large tree. Such trees are a common feature in roosting and especially nesting areas used by Mexican spotted owls.

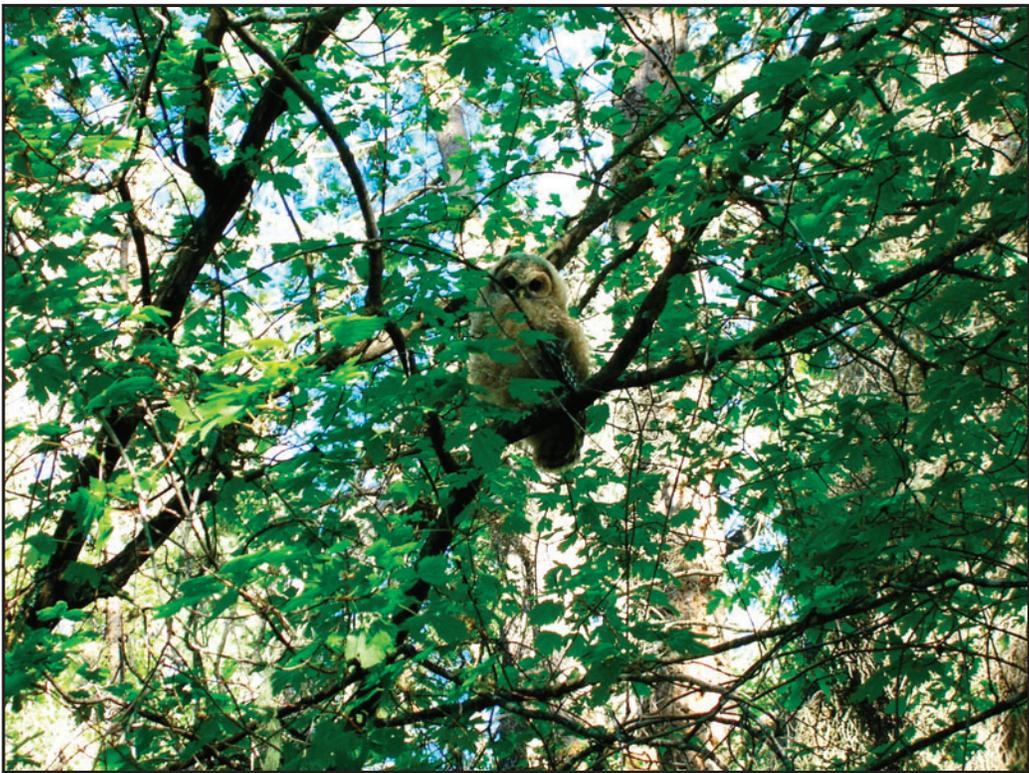


Figure 17. A pair of Mexican spotted owls in a Gambel oak tree (top) and a juvenile Mexican spotted roosting in hardwood foliage (bottom). Hardwood foliage provides additional structural complexity in roost and nest areas, canopy layering, shade during summer, and cover from predators. Photos: Niki vonHedemann (top), Todd A. Rawlinson (bottom).

Reasons Underlying Habitat-Selection Patterns

Several possible mechanisms underlie observed patterns of habitat use and selection by Mexican spotted owls. For example, several hypotheses have been proposed to explain why spotted owls nest and roost in late-seral, closed-canopy forests (reviewed by Carey 1985, Gutiérrez 1985). These include better thermal protection, greater access to prey, protection from predation, and availability of required nesting structures. Information documenting the relative importance of these factors is limited, with the exception of information relating to thermal and prey ecology.

Barrows (1981) suggested that spotted owls are relatively intolerant of high temperatures and roost and nest in shady forests because they provide favorable microclimatic conditions. This explanation seems particularly attractive with respect to Mexican spotted owls, because it provides a unifying explanation for the use of extremes along the occupied habitat gradient. Both closed-canopy forests and deep rocky canyons with caves, potholes, and alcoves provide well-shaded and cool microsites relative to surrounding areas, and owls typically use such areas for roosting and nesting (for example, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Rinkevich and Gutiérrez 1996, Willey 1998a, Ganey and others 2000, May and others 2004, Willey and Ward 2004).

There is empirical evidence in support of the thermal hypothesis in addition to observed patterns of habitat use. Mexican spotted owls produce more metabolic heat than great horned owls, and are less able to dissipate that heat through evaporative cooling (Ganey and others 1993). In addition, studies of California spotted owls show that rates of water flux also are high relative to metabolic rates (Weathers and others 2001), suggesting that minimizing water loss might contribute to the owls' selection of habitats. Thermal environments of Mexican spotted owl nest areas sampled are significantly cooler than paired random areas during the summer, and estimated evaporative water loss by Mexican spotted owls was significantly lower in nest than in random areas (Ganey 2004).

Potentially conflicting with this hypothesis is the presence of Mexican spotted owls in canyons and riparian areas at relatively low elevations (for example, Willey and Ward 2004). Although owls appear to select microsites in these canyons that are cooler than surrounding areas, summer daytime temperatures can be quite warm. Owls may be able to maintain favorable water and energy balance even in warm environments if water and prey resources are readily available in sufficient quantities. The ultimate quality of these sites is unknown, as both vital rates of owls using such sites and availability of prey resources in these sites remain unknown.

Taken together, the above research findings suggest that thermal environments may be important in shaping patterns of habitat selection by Mexican spotted owls but do not rule out other explanations. The same types of structural features that result in cooler microclimates may be correlated with factors such as prey abundance, protection from predators, or availability of nest structures. For example, relatively dense forests with closed canopies and high basal area may provide

improved hiding cover for owls in general, especially for inexperienced juvenile owls. Hardwoods may be particularly important in this regard. Such forests also may provide more and better den structures for small mammals, as well as large, decadent trees that provide suitable nest structures for owls. Similarly, canyon bottoms may be more productive sites for the owl's prey in northern regions of the owl's range (Sureda and Morrison 1998). Owls that select roosting and nesting sites in proximity to other required resources will presumably save energy in acquiring those resources, spend less time away from young, and potentially decrease risk of detection by predators. It seems unlikely that habitat selection is based solely on thermal constraints, and more likely that such constraints interact with other factors (see also Carey and others 1992, Zabel and others 1995, Ward and others 1998, Ward 2001, May and others 2004).

Disturbance Ecology and Owl Habitat

Several disturbance factors can influence Mexican spotted owls through their effects on the owl's habitat. For example, a change-detection analysis focused on Mexican spotted owl habitat (Mellin and others 2000) suggested that wildland fire, mechanical treatments, and forest insects and pathogens (in that order) were key disturbance agents affecting owl habitat between 1991 and 1998. Other potential disturbance agents that may threaten the owl indirectly through habitat alteration include excessive grazing by domestic livestock and/or wild ungulates, concentrated housing development or urbanization, and shifts in the distribution of dominant plants and their associations driven by change in climate. All of these disturbance agents may alter habitat structure, reducing the quality or availability of habitat to individual owls.

No studies are available on the specific effects of forest insects and pathogens on this owl's habitat, or on the effects of mechanical treatments on Mexican spotted owls. As a result we know relatively little about the effects of these disturbance agents. Several studies or analyses have focused on wildland fire, and this disturbance agent has the potential to alter the owl's habitat rapidly. For example, Sheppard and Farnsworth (1997) estimated that at least 10 Mexican spotted owl territories were impacted by fire in Arizona and New Mexico during the 1994 fire season alone, and that >50,000 ac (20,000 ha) of owl habitat experienced stand-replacing wildfire from 1989 to 1994. More recently, Williams and others (2010) estimated that at least 2.7–3.0% of Southwestern forest and woodland area was affected by stand-replacing wildland fire between 1984 and 2006, and that the annual fraction of area affected by severe fire increased substantially over that period. Therefore, this disturbance agent and its potential influence on the ecology of Mexican spotted owls warrants specific discussion. There also is limited information about three other disturbances that may influence the owl's habitat: grazing by domestic livestock and wild ungulates, urban development, and shifts in biological communities caused by climate change. Below, we briefly discuss the potential influences of these four disturbance agents.

Wildland and Prescribed Fire—Fire historically was a major disturbance agent in Southwestern forests (Swetnam 1990), and Mexican spotted owls co-evolved with this disturbance. Fire regime varied both among and within Southwestern forest types occupied by Mexican spotted owls. For example, fire regime generally was more variable in mixed-conifer forests (Dieterich 1983, Fulé and others 2002, 2003, 2004, 2009, Cocks and others 2005, Kaufman and others 2007) than in ponderosa pine forests (Cooper 1960, Covington and Moore 1994, Fulé and others 1997, Kaufmann and others 2007), and fire return intervals were variable within mixed-conifer forests (Fulé and others 2003). Fire return intervals in many dry mixed-conifer types were similar to those in ponderosa pine forests, whereas mesic mixed-conifer forests had longer return intervals and more of a mixed- than a low-severity fire regime (Fulé and others 2003). Despite this variation, the structure of many forested areas within the UGM RU, the frequency with which they experience fire, and the types of fires experienced have changed greatly following increased human settlement of these lands (Covington and Moore 1994, Fulé and others 1997, 2004, 2009, Cocks and others 2005). These forests, especially ponderosa pine and the drier mixed-conifer forests, evolved with a fire regime characterized by relatively short return intervals, but effective fire-suppression activities disrupted that cycle. As a result, many of these areas have not experienced fire for long intervals. Effective fire suppression and heavy grazing in combination also favored the development of dense stands featuring multiple age classes of trees and heavy loads of ground fuels (Rummel 1951, Madany and West 1983, Savage and Swetnam 1990, Covington and Moore 1994, Fulé and others 2004, 2009). These changes in fire frequency and forest structure affect fire behavior. Forests that once were subject to relatively frequent, low-severity wildland fires are now more prone to infrequent, high-severity wildland fires (Fulé and others 2004). These fires are far more likely to reach the forest canopy than in historical times, due to the presence of heavy ground fuels and fuel ladders reaching into the canopy. Once fire reaches the canopy, it becomes very difficult to contain, resulting in a trend toward increasing size and severity of wildfires in the Southwest in recent years (USDI FWS 1995:60–61; see also Williams and others 2010).

Recognizing these aspects of Southwestern forest ecology, USDI FWS (1995:82) explicitly recognized stand-replacing wildland fire as one of the primary threats to the owls and their habitat and emphasized that fire management aimed at reducing heavy fuel loads should be given high priority. The underlying assumption was that stand-replacing wildland fire would destroy the aspects of stand structure that spotted owls utilize for roosting and nesting. Understanding the impact of wildland fire on Mexican spotted owls requires knowledge of the owl's response to fire, however.

Several studies have examined short-term effects of fire on Mexican spotted owls in the UGM RU. Bond and others (2002) documented minimum survival and site and mate fidelity for four pairs of color-marked Mexican spotted owls in Arizona and New Mexico after large wildland fires (>1300 ac [525 ha]). Fire burned through the nest and primary roost sites in all four territories. Two territories experienced high-severity wildland fire over >50% of the territory, one experienced relatively high-severity fire over approximately 40% of the territory, and one experienced

primarily low-severity wildland fire. Seven owls (87.5%) were known to have survived at least to the next breeding season. Three of the four pairs exhibited both mate and site fidelity, remaining paired and on the same territory. The male from the fourth territory was not re-sighted, and the female survived but did not return to that territory. This territory underwent the greatest burn severity, experiencing high-severity wildland fire over 57% of the territory and low-severity wildland fire over the remaining 43%. Thus, owls studied continued to occupy some burned areas, even following relatively high-severity fires, and mate and site fidelity in these owls were relatively high in the year following fire.

Jenness and others (2004) surveyed historical Mexican spotted owl territories (as delineated by USFS biologists) in 1997 that had experienced some form of fire during the previous four years, and compared owl occupancy and reproduction in these territories to unburned territories that were located nearby and were similar in cover type and topography. They surveyed 33 burned territories and 31 unburned territories in the Upper Gila Mountains, Basin and Range–West, and Basin and Range–East Recovery Units. Extent and severity of fire within these territories varied widely, ranging from prescribed burns to intense wildland fires that burned across much of the territory.

In general, unburned territories surveyed had more pairs (55%) and reproductive pairs (16%) than burned territories (39 and 9%, respectively). Burned territories were more likely to contain single owls than unburned territories (21 vs. 16%) and almost twice as likely to be unoccupied (30 vs. 16%). These differences were not statistically significant, but the significance test had low power due to small samples of sites (Jenness and others 2004). Two of eight territories (25%) that burned one year prior to surveys were unoccupied, and eight of 25 territories (32%) that burned ≥ 2 years prior to surveys were unoccupied. Owls were present and reproducing in some severely burned sites, however. For example, 3 sites where $>50\%$ of the territory burned contained reproducing pairs, and a single owl was present at the most severely burned territory. These results also suggest that owls frequently continue to occupy burned areas, at least in the short term, and that some burned areas continue to be occupied even after severe, stand-replacing wildland fires. None of the burned territories had $>55\%$ stand-replacing burn within the territory boundary delineated by USFS, so pockets of habitat remained in all cases. Further, because owls were neither radio- nor color-marked in this study, it is not known if the birds present after fires were the same birds present before the fires.

In addition to these studies, there are studies of Mexican spotted owls and fire in other areas (for example, Willey 1998b) and numerous anecdotal observations that document Mexican spotted owls occupying territories following wildland fires and prescribed burns (Paul Boucher, Gila National Forest retired, pers. comm.; Shaula Hedwall, USFWS, pers. comm.). There also is evidence of radio-marked owls remaining on burned territories following wildland fire (Peter Stacey, University of New Mexico, pers. comm.), or moving into and foraging in burned areas during winter (J. P. Ward and J. L. Ganey, unpublished data). Most wildland fires burn in a patchy nature and leave pockets of useable habitat for owls, and owls

appear able to locate and use these patches. Thus, Mexican spotted owls appear to be somewhat resilient to wildland fire, at least in the short term. We have no data on long-term effects of these fires on occupancy patterns, or on components of Mexican spotted owl fitness such as survival and reproduction. Further, the effect of fire likely varies greatly with spatial pattern. That is, fires that burn most of a territory likely have a greater effect than fires that burn only portions of a territory, and fires that burn in a patchy mosaic likely have less effect than fires that burn with high severity throughout a territory. Similarly, fires that burn favored roosting and nesting habitat likely have a greater effect than fires that burn only foraging habitat. In fact, fire may result in good foraging habitat, at least in the short term (Bond and others 2009). Finally, spotted owls in general show high site fidelity (Gutiérrez and others 1995). Because of this, owls might continue to occupy burned territories even if habitat quality was degraded considerably. Thus, long-term data on owl demography, with information on the spatial pattern of fire severity and owl habitat use, will be required to fully understand the effects of fire on spotted owls.

Grazing—Intensive grazing by domestic livestock and wild ungulates can influence both tree regeneration and dynamics and composition of the understory vegetation that provides cover and food to the owl's prey in forests occupied by owls. No studies have evaluated effects of grazing on spotted owls in the UGM RU, and only one study has specifically addressed effects of grazing on Mexican spotted owls. This study found that both woodrat abundance and overall small mammal species diversity were greater in ungrazed than in adjacent grazed transects in two owl territories in the canyonlands of southern Utah (Colorado Plateau RU; Willey and Willey 2010).

There also is circumstantial evidence that grazing may affect prey abundance and thus indirectly affect owls. For example, species such as voles are highly dependent on herbaceous plants for cover, food, and water (for example, Ward 2001, Chambers and Doucett 2008, Kalies and Chambers 2010) and may be impacted where grazing reduces herbaceous cover. These species can provide important contributions to owl diets in some regions and years (Ganey 1992, Ward and Block 1995, Seamans and Gutiérrez 1999, Ward 2001). Hence, grazing could negatively influence owl abundance indirectly by decreasing populations of key prey species, which in turn can reduce owl survival and reproduction. Given the widespread extent of grazing on public lands, and our limited knowledge, this is an area deserving of further research.

Grazing also can affect forest structure, particularly by influencing patterns of tree regeneration. This has occurred in both upland (Rummel 1951) and riparian forests, but it likely is most important in riparian forests (Stacey and Hodgson 1999). Mexican spotted owls at one time nested in lowland cottonwood bosques in parts of their range (Bendire 1892, Bailey 1928, Phillips and others 1964). Most of these areas have been heavily impacted by grazing, and there are no recent records of spotted owls occupying such areas. Riparian forest along major rivers in the Southwest also may provide Mexican spotted owls with movement corridors in a landscape that otherwise might prove resistant to effective movement or dispersal.

Montane riparian systems also have been impacted by grazing. Stacey and Hodgson (1999) noted that canyon-bottom riparian habitats in the San Mateo Mountains, New Mexico, differed between areas inside and outside of livestock exclosures. Within the exclosures, canyon bottoms supported dense stands of narrowleaf cottonwood, willows, and other riparian species. In contrast, areas outside of the exclosures contained some remnant riparian vegetation, but cottonwoods were not regenerating and most had died.

In another example, Martin (2007) documented significant declines in abundance of deciduous trees in snowmelt drainages along the Mogollon Rim, Arizona (within both the UGM RU and the 4FRI area) between 1987 and 2007. He attributed much of this decline to increased browsing pressure by elk. That increase in turn was facilitated by warmer winters and reduced snowpack, which allowed elk to remain in the area during winter months rather than migrating to lower elevations. The observed changes in forest structure and composition were significant enough to cause the local extinction of one formerly common bird species and severe population declines in several other species. Similar impacts may have occurred elsewhere in montane riparian systems within the UGM RU.

Urbanization—Urbanization and land development can affect Mexican spotted owls both directly and indirectly. Development and urbanization can affect owls directly where suitable habitat is lost, or indirectly through effects on either ecological integrity or management practices. Development impacts also may vary by area. In some areas spotted owls occur in landscapes with small amounts of private land, whereas other populations occur in landscapes with far greater amounts of private land. Development impacts likely will be greater in landscapes with larger amounts of private land, and some forms of development may have greater impacts than others. Development impacts also may depend on spatial location. Development in suitable nesting habitat may be more detrimental than development in foraging habitat at the periphery of a home range, and development in key stepping-stone or wintering areas (see sections on **MOVEMENTS AND MIGRATION** and **META-POPULATION ECOLOGY**) may be more detrimental than similar development in areas that are not as important spatially. Finally, development can exert indirect impacts by affecting management policies and decisions. For example, managers may more aggressively reduce forest fuels and canopies in areas adjacent to private lands than in more remote areas, and these activities may impact habitat quality for Mexican spotted owls.

No studies have directly examined the effects of land development on Mexican spotted owls, so the extent of potential impacts remains unknown. Impacts may be significant, however. An analysis of the effects of interspersed urban land development on the amount and availability of habitat suitable for California spotted owls demonstrated that such development could reduce the amount of suitable habitat by more than 50% over a 40-yr period (Manley and others 2009). Given that federal land managers have no control over development on private lands, this suggests that federal lands are particularly important for sustaining owl habitat and populations.

It further suggests that areas lacking significant amounts of private inholdings may be best suited to maintaining contiguous forest habitat for owls, assuming that such areas contain the appropriate cover types.

Climate Change—Climate change is the shift in previous long-term and wide-ranging patterns in meteorological parameters that are used to characterize weather. Climate and resulting weather patterns drive most ecological processes. The emerging phenomenon of climate change has the potential to impact Mexican spotted owls in three general ways: (1) directly, through impacts on key physiological processes like thermoregulation and water balance, (2) indirectly, through similar impacts on desired prey species, and (3) indirectly, by causing shifts in physical limits that control distribution of other animal or plant species that create biological communities that influence the owl. Mawdsley and others (2009) categorized these effects more specifically as: (1) shifts in the distribution of biological communities along elevational or latitudinal gradients; (2) direct loss of habitat due to increased fire frequency, bark beetle outbreaks, and direct warming of habitats; (3) effects on demographic rates, such as survival and reproduction; (4) reductions in population size; (5) changes in coevolved interactions, such as predator-prey relationships; and (6) increased abundance of or range expansion by species that are direct competitors.

Climate change may be the biggest issue facing Mexican spotted owls. It has the potential to affect spotted owl vital rates directly (for example, Seamans and others 2002, Glenn and others 2010) and to cause profound and rapidly occurring changes in the forests occupied by these owls (for example, Ganey and Vojta 2010, Williams and others 2010). Unfortunately, the science on ecological effects of climate change is just beginning to emerge, and no empirical data are available on the effects of climate change on Mexican spotted owls. Thus, assessments of the effects of climate change on Mexican spotted owls at this time necessarily are speculative, based on circumstantial information, and beyond the scope of this report.

Habitat Modeling Efforts

Several efforts have been made to develop predictive models for Mexican spotted owl habitat within the UGM RU. These efforts and the resulting models are discussed below.

Ganey and Benoit (2002) evaluated the use of Terrestrial Ecosystem Survey (TES) data to identify potential spotted owl habitat on National Forest System lands. TES is a spatially explicit data set that uses information on soils, vegetation, and climatic conditions to define and map a set of ecological Map Units depicting potential vegetation. Using three separate owl data sets (locations from the 1993 agency survey database [USDI FWS 1995], locations of radio-marked owls [Ganey and Balda 1989b, Ganey and others 1999], and results from complete surveys of

selected quadrats [Ganey and others 2004]), they identified subsets of map units that were strongly associated with owl use on three (Apache-Sitgreaves, Coconino, and Kaibab [Williams Ranger District only]) National Forests within the 4FRI area in northern Arizona.

The identified map units generally consisted of mixed-conifer or pine-oak forest, and those most strongly associated with owl use generally occurred on steep (>40%) slopes containing rocky outcrops. Most map units strongly associated with owl use fell in the Low Sun–Cold climate class as defined by TES (USDA FS 1986). Most also fell within climate zones typical of ponderosa pine and mixed-conifer forests (zones 5 and 6; Ganey and Benoit 2002: Table 10). Map units occurred across the full climatic range within these zones, but a high proportion of map units fell towards the warm, dry end of the mixed-conifer zone (Ganey and Benoit 2002: Table 10). Some of the habitat thresholds (see **Habitat Characteristics of Areas Used By Owls, Stand Scale**) suggested by studies of habitat use by radio-marked owls in mesic mixed-conifer forest may not be appropriate in these warmer, drier mixed-conifer types.

Many of the map units identified either provided no information on suitability for timber harvest, suggesting that harvest was not a management priority in these units, or were classified as presenting severe limits to timber harvest (Ganey and Benoit 2002: Table 10). This often was due to steep slopes, but soil considerations also limited suitability for harvest in some map units. In terms of spatial extent, map units strongly associated with owl use comprised 23.3, 23.8, and 7.6% of total area within the Apache-Sitgreaves, Coconino, and Kaibab National Forests, respectively (fig. 18). The markedly lower proportion of map units associated with owl use on the Kaibab National Forest appears consistent with results from agency surveys, which have located few owls on that forest (see fig. 7).

Ganey and Benoit (2002) concluded that, with some caveats, TES data could be used to identify and map potential owl habitat. They also recommended that initial habitat management efforts for spotted owls should focus on the suite of map units identified as associated with owl use. Spatial coverages resulting from this study were provided to Forest Biologists and are available to 4FRI planners as well.

Mellin and others (2000) evaluated the feasibility of assessing gross changes in amounts of spotted owl habitat over time (in other words, change detection). They identified forest types associated with spotted owls on National Forest System lands in Arizona and New Mexico, using TES (see above) and Generalized Ecosystem Survey data (essentially a coarser-scale version of TES), and USFS timber stand data. They then assessed changes within those vegetation types using two Landsat images acquired approximately five years apart (1991/93 and 1997/98; Mellin and others 2000). Thus, this modeling effort included the UGM RU but was not restricted to that RU.

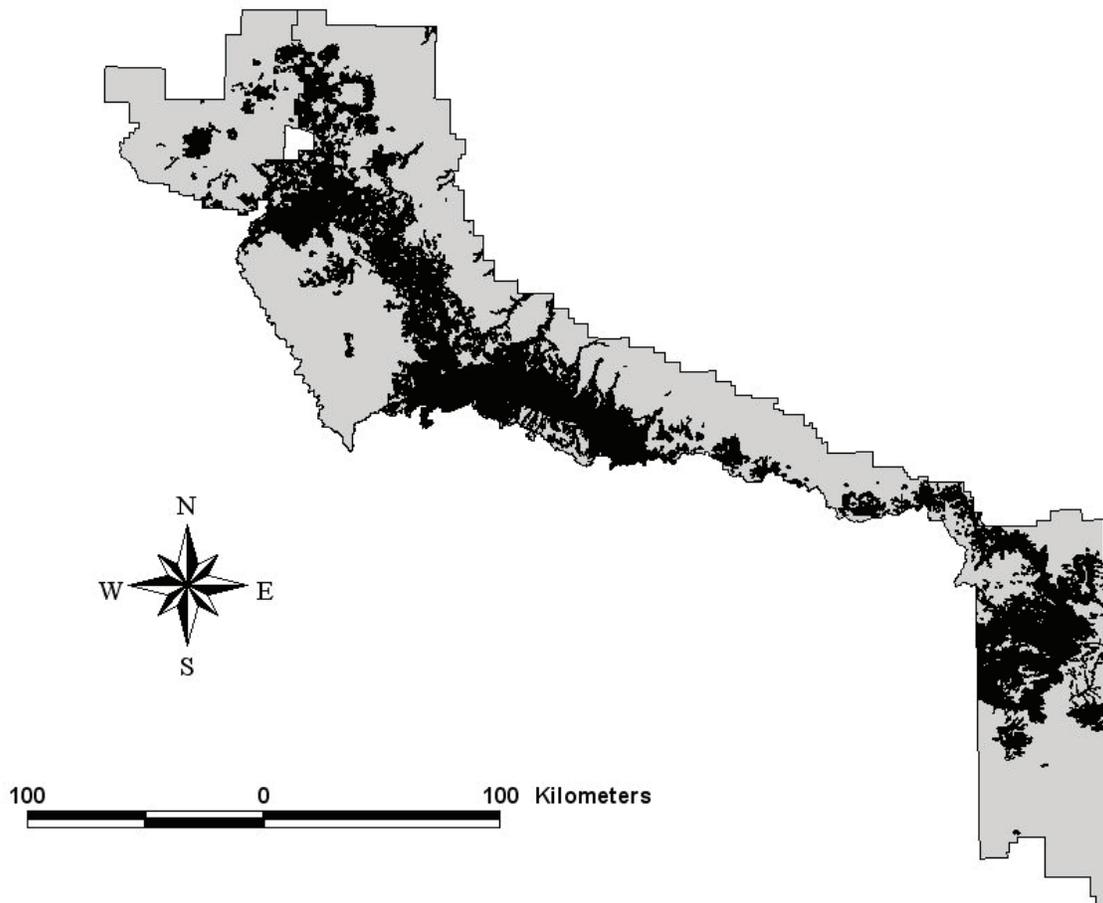


Figure 18. Spatial distribution of Terrestrial Ecosystem Map Units identified as strongly associated with Mexican spotted owls (shaded areas) in the Kaibab, Coconino, and Apache-Sitgreaves National Forests, Arizona. From Ganey and Benoit (2002: Figure 4).

Approximately 28.2% of National Forest System lands within Arizona and New Mexico were identified as belonging to vegetation units associated with spotted owls. Within those vegetation units, 4.2% underwent some form of vegetation removal or reduction over the 5-yr period, for an annual rate of change of <1%. Region-wide, fire was the principal cause of habitat change identified and accounted for 60.5% of the change area. Timber harvest accounted for another 19.2%, with infestations of forest insects or pathogens accounting for 17.3% of the change area (Mellin and others 2000: Figure 5.)

Within the UGM RU, proportion of forest area in vegetation units associated with spotted owls varied among forests, and percent change within owl-associated vegetation units generally was relatively low (Table 11). Causes of change within these vegetation units also varied among forests. Timber harvest was the primary agent of change during this time period on the Apache-Sitgreaves, Coconino, and Kaibab National Forests. In contrast, fire was the primary agent of change in the Cibola, Gila, and Tonto National Forests (Table 11).

Table 11. Proportion of National Forests within the Upper Gila Mountains Recovery Unit comprised of vegetation units associated with spotted owls, as identified by Mellin and others (2000). Also shown are proportions of those vegetation units that underwent detectable change in status between 1991/93 and 1997/98, and the primary agent causing that change in status. Source: Mellin and others (2000: Figures 6 and 7).

National Forest	% area associated with owl use	% change in areas associated with owl use	Primary cause of change
Apache-Sitgreaves ¹	41.4	3.1	Timber harvest
Cibola ¹	35.5	1.2	Fire
Coconino	36.0	6.2	Timber harvest
Gila	48.3	3.8	Fire
Kaibab ¹	10.4	5.2	Timber harvest
Tonto ¹	17.7	1.5	Fire

¹ Parts of these forests occur outside of the Upper Gila Mountains Recovery Unit, but data was not summarized by Recovery Unit.

This modeling effort demonstrated that Landsat imagery could be used to detect gross changes in habitats over time, as recommended in USDI FWS (1995). Thus, continued change-detection efforts could form part of a strategy to monitor trend in amounts and spatial distribution of owl habitat. However, the change-detection analysis focused mainly on obvious loss or reduction in vegetation. Identifying areas that may have matured toward suitable owl habitat during this time frame was beyond the scope of this effort but obviously would be important in a comprehensive effort to monitor trend (including both gains and losses) in owl habitat.

Another modeling effort was conducted in this area by the Forest Ecosystem Restoration Analysis (ForestERA) program, a collaborative project headquartered within the Center for Environmental Science and Education at Northern Arizona University. ForestERA provides data, tools, and analytical frameworks for developing landscape-level strategies for ecosystem restoration and assessing the impacts of alternative management scenarios (Hampton and others 2003, Sisk and others 2006) and is actively assisting 4FRI planners.

ForestERA developed a predictive model for Mexican spotted owl habitat covering a study area of approximately 2 million ac (810,000 ha) near Flagstaff, Arizona (fig. 19; Hampton and others 2003, Prather and others 2008). This area was contained within the 4FRI boundary. The model defined spotted owl nesting and roosting habitat as areas within mixed-conifer or pine-oak forest where basal area exceeded $75 \text{ ft}^2 \text{ acre}^{-1}$ ($17 \text{ m}^2 \text{ ha}^{-1}$), or areas in ponderosa pine on steep ($>8^\circ$) slopes with basal area $>75 \text{ ft}^2 \text{ acre}^{-1}$ (Prather and others 2008). The model classified 26.7% of the assessment area as nest/roost habitat, but these areas captured 85% of 132 nest and roost sites contained within the assessment area (Prather and others 2008).

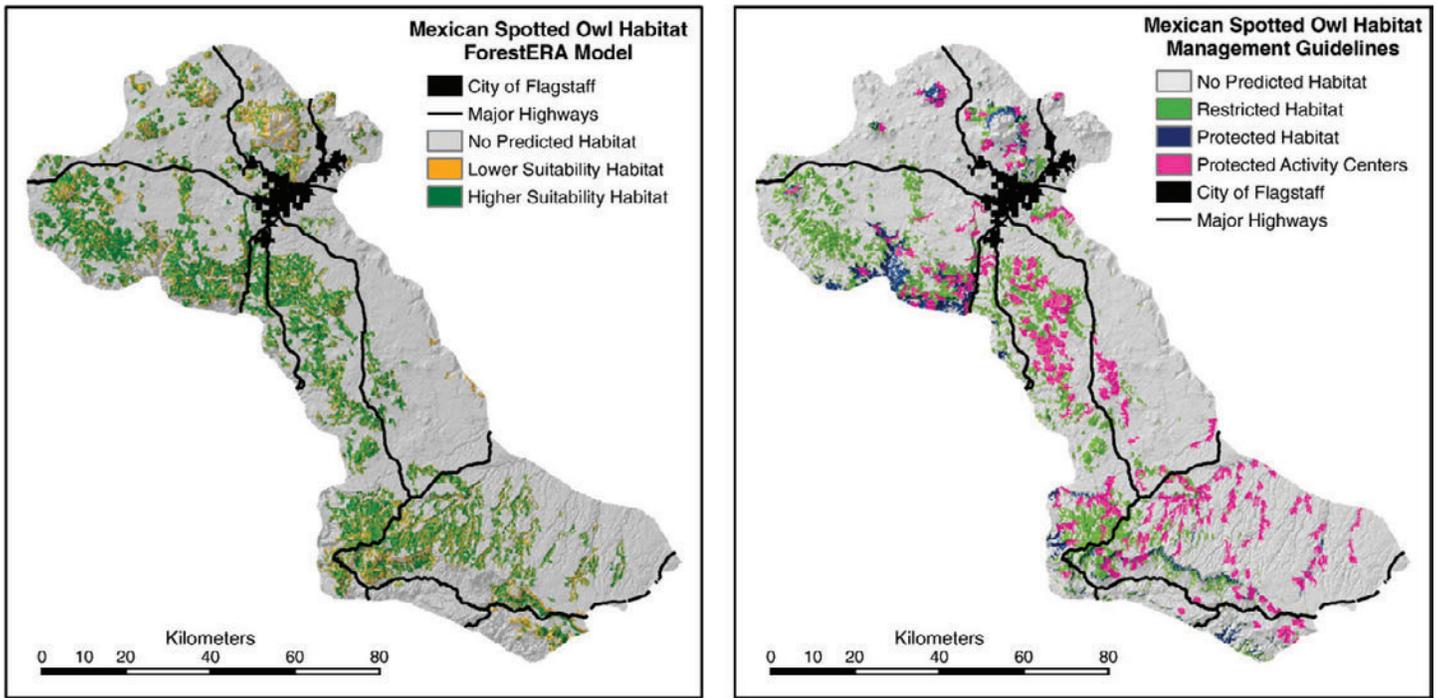


Figure 19. Map of Mexican spotted owl habitat as predicted by the ForestERA model (left), and areas predicted to fall in various management categories (right) defined in USDI FWS (1995). Reprinted from Prather and others (2008: Figure 1) with permission from Elsevier.

ForestERA also produced a second spatial coverage representing management definitions of Mexican spotted owl habitat across the assessment area (fig 19). This data layer depicted habitat categories as defined in USDI FWS (1995), including protected habitat, restricted habitat, and areas with no specific owl-related guidelines (other forest and woodland types; USDI FWS 1995). This layer identified 20.9% of the analysis area as either protected or restricted habitat. Finally, they created a third spatial layer consisting of PAC boundaries obtained from USFS. PACs comprised 8.0% of the analysis area. Overlap between areas defined as nesting and roosting habitat by the model and areas managed as protected and restricted habitat generally appeared to be high (fig. 19).

Prather and others (2008) used this model to evaluate potential conflicts between management to reduce fuels and risk of severe wildfire and management to retain spotted owl habitat. They concluded that the magnitude of conflicts between these objectives has been overstated, and that the majority of the landscape could be managed to reduce fire hazard without eliminating owl habitat (see James 2005 for a concurring view).

A number of other investigators have developed models for owl habitat covering other regions within the range of the Mexican spotted owl (for example, Johnson 2003, Danzer 2005, Willey and others 2007, Hathcock and Haarmann 2008, Mullet 2008). A number of these efforts have emphasized use of topographic and/or climatic data that is readily available for all land ownerships across the range of the owl, and many have been successful in predicting where owls would be located in subsequent surveys. In general, models incorporating topography appear to hold

the most promise for modeling owl habitat in areas such as rocky canyonlands, where topography and geology appear more important in determining owl distribution than vegetation type. In some areas, data on vegetation type and composition may improve models significantly. These types of data are not as readily available as topographic data and typically require analysis of satellite imagery to derive useful data layers at large spatial scales. Such data can be used to detect changes in vegetation structure (for example, Mellin and others 2000), however, and this ability would appear to be critical in efforts to monitor amounts and distribution of spotted owl habitat in forested areas.

Demography and Life History

Although Forest Service managers do not manipulate populations of native wildlife directly, understanding how and why populations change over time is fundamental for informed conservation planning. Only two studies have evaluated demographic trends in Mexican spotted owl populations within the UGM RU (Seamans and others 1999, Stacey and Peery 2002), and both studies were conducted in the 1990s. Consequently, we have no current information on population trends in this RU, and historical data are sparse.

Both studies used Leslie stage-projection matrix models to estimate population trend. Seamans and others (1999) reported declining populations for two study areas in Arizona and New Mexico (Table 12), and their model-based trend estimates also were supported by count-based estimates of owl abundance from 1992 to 1997 (Seamans and others 1999: figure 4). Stacey and Peery (2002, see also Stacey 2010: Table 35.1)

Table 12. Characteristics of study areas and estimates of population trend from mark-recapture studies of Mexican spotted owls within the Upper Gila Mountains Recovery Unit. U = unknown; data not reported.

Characteristic	Study area ¹				
	CNF	GNF	BR	SMM	MM
Land area	226 mi ² 585 km ²	125 mi ² 323 km ²	U	U	U
Major cover types (%)					
Mixed-conifer	14.4	28.5	U	U	U
Pine-oak	82.2	30.8	U	U	U
Pinyon-juniper woodland/grassland	3.4	40.7	U	U	U
Years studied	1991-98	1991-98	1991-99	1991-99	1991-99
Number of owl territories ²	18–44	18–32	U	U	U
Rate of population change ³ :					
Mean	0.896	0.857	0.841	0.695	NA ⁴
Standard error	0.055	0.029	0.05 ⁵	0.10 ⁵	NA ⁴
Sources ⁶	1	1	2	2	2

¹ Acronyms for study areas: CNF = Coconino National Forest, AZ; GNF = Tularosa Mountains, Gila National Forest, NM; BR = Black Range, Gila National Forest, NM; SMM = San Mateo Mountains, Cibola National Forest, New Mexico; MM = Magdalena Mountains, Cibola National Forest, New Mexico. Study areas are described further in Appendix 2.

² Range across years shown.

³ Interpretation: values <1.0 indicate declining populations, with the magnitude of the decline proportional to the departure from 1.0

⁴ Population under study reportedly declined to zero.

⁵ Estimate of variability not specified in source; may be standard error or standard deviation.

⁶ Sources: 1 = Seamans and others 1999; 2 = Stacey and Peery 2002.

reported declining trends in owl populations in the Black Range and San Mateo, and Magdalena Mountains, UGM RU (Table 12; see also Appendix 2), as well as in the Zuni Mountains located in the adjacent Colorado Plateau RU. Declining trends also were evident when populations from these four mountain ranges were combined for analysis (overall $\lambda = 0.803$, 95% confidence interval = 0.73 to 0.89, Stacey and Peery 2002; λ is an index of population change, with values <1 indicating a declining population). Populations in the Zuni and Magdalena Mountains apparently declined to zero during the study. Some re-colonization occurred in both ranges, but the populations were unstable, with territories typically occupied for only a year or two before becoming vacant again (Stacey 2010). Thus, available studies indicate that all populations studied were declining during the 1990s.

Reproductive Biology and Rates

Mexican spotted owls breed sporadically and do not nest every year (Gutiérrez and others 1995, White and others 1995, Stacey 2010). In good years, much of the population will nest, whereas in some years only a small proportion of pairs will nest successfully (Gutiérrez and others 1995). Reasons for this pattern of sporadic breeding are unknown, but temporal variation in food resources and weather are suspected to influence both the proportion of pairs nesting and the proportion fledging young.

Annual reproductive output of Mexican spotted owls, defined as the number of young fledged per pair, varies spatially, temporally, and by age-class (Seamans and others 1999, 2002). Similar to other spotted owl subspecies, average reproductive rates are generally low in Mexican spotted owl populations, and adult owls usually have higher reproductive rates than subadults (Table 13; see also Seamans and others 2002). Temporal variation in reproductive rate is pronounced in Mexican spotted owls. For example, reproductive output over an eight-year period varied from 0.44 to 1.70 and from 0.10 to 1.47 young fledged per territorial female in study areas in Arizona and New Mexico, respectively (Seamans and others 2002).

Table 13. Age-specific annual reproductive output (young fledged pair⁻¹) of Mexican spotted owls within the Upper Gila Mountains Recovery Unit, 1991 through 1997. Recalculated from fecundity data in Seamans and others 1999: Table 1.

Study area ¹	Age-class	N ²	Mean	SE
CNF	1-yr-olds	9	0.222	0.222
	≥2-yr-olds	158	0.988	0.086
GNF	1-yr-olds	6	0.000	0.000
	≥2-yr-olds	138	0.760	0.074

¹ Study area acronyms: CNF = Coconino National Forest, Arizona; GNF = Tularosa Mountains, Gila National Forest, New Mexico. Study areas are described further in Appendix 2.

² Number of females checked for reproduction within age class.

Survival Rates

Annual survival is defined as the probability of an individual surviving from one year to the next, or as the proportion of individuals in a population that will survive from one year to the next. Survival rates of spotted owls typically are estimated either by marking individuals with leg-bands (fig. 20) and documenting their presence through re-sighting in a spatially explicit population through multiple years (for example, Franklin and others 1996), or by intensively monitoring fates of radio-marked owls over shorter periods of time. Survival estimates for Mexican spotted owls within the UGM RU are fairly comparable between techniques and generally indicate relatively high survival rates for adult owls, intermediate survival rates for subadult owls, and relatively low survival of juvenile owls (Table 14). This pattern also has been observed in the better-studied northern (Burnham and others 1996, Anthony and others 2006) and California (Franklin and others 2004, LaHaye and others 2004) subspecies of spotted owls. However, temporal variation in survival rates appears to be greater in Mexican spotted owls (Seamans and others 2002: Figure 3) than in the other subspecies.

Environmental Variation and Vital Rates

Conservation of wildlife populations requires information about the factors that influence vital rates and ultimately population growth. Only one study of two Mexican spotted owl populations has rigorously examined sources of variation in survival and reproduction within the UGM RU (Seamans and others 2002). This study indicated that owl survival in the New Mexico study area (GNF) and reproductive rates in both areas were positively influenced by precipitation. In Arizona (CNF), precipitation from the previous year explained 73% of temporal variation in reproductive output, and precipitation from the previous monsoon season explained 53% of the temporal variation in survival. In New Mexico, precipitation from the previous monsoon explained 42% of temporal variation in reproductive output, and precipitation from the previous winter explained 56% of temporal variation in owl survival. For both study areas, reproductive output varied more than survival across years.

Effects of Habitat on Vital Rates

No published studies have evaluated the effects of habitat composition or configuration on vital rates of Mexican spotted owls within the UGM RU. A study in the Sacramento Mountains, New Mexico (Basin and Range-East RU, Ward 2001) found that reproductive output of spotted owls was influenced by abundance of smaller rodents such as mice and voles in mixed-conifer forests. Abundance of these same prey species in two other cover types (montane meadow and xeric forest) had little influence. Temporal variability in abundance of these rodents was greater than spatial variability among cover types. That is, rodent abundance varied more among years than among cover types within year.



Figure 20. A banded Mexican spotted owl in hand (top) and another taking flight (bottom). Visible in the top photo are the numbered metal US Fish and Wildlife Service band and a plastic colorband (color band combination =blue/red). Note that the color band is visible in the bottom photo (black/white, left leg), as well as the metal US Fish and Wildlife Service band (right leg). These color bands can be used to uniquely identify individual owls in subsequent resightings, which eliminates the need to recapture the owl to identify individuals. Sighting histories across years can be used to estimate apparent annual survival. Bottom photo by Niki vonHedemann.

Table 14. Estimates of age-specific annual survival for Mexican spotted owls within the Upper Gila Mountains Recovery Unit. *N* = number of owls included in estimate.

Study area(s) ¹	Age-class	Survival estimate			Source ²
		<i>N</i>	Mean	<i>SE</i>	
CNF	≥1-yr-olds	72	0.814	0.050	1
GNF	2-yr-olds	21	0.644	0.048	1
GNF	≥3-yr-olds	126	0.832	0.029	1
SFP, WM, WC	≥2-yr-olds	8	0.880	0.120	2
BMC	≥2-yr-olds	13	0.790	0.100	2
CNF	<1-yr-olds	124	0.230	0.064	1
GNF	<1-yr-olds	115	0.080	0.028	1
CNF	<1-yr-olds	25	0.205-0.287 ³	0.028	3

¹ Study area acronyms: CNF = Coconino National Forest, Arizona; GNF = Tularosa Mountains, Gila National Forest, New Mexico. Study areas are described further in Appendix 2.

² Source: 1 = Seamans and others (1999, based on mark-recapture estimates); 2 = calculated from unpublished data on radio-marked owls; see Ganey and others (1989b, 1999); 3 = Ganey and others (1998, based on radio-marked owls).

³ Estimate differed depending on whether or not owls that were suspected to be dead were included as mortality events or censored.

Working in this same mountain range, Lavier (2006) evaluated the influence of environmental factors on extinction and colonization rates of Mexican spotted owl territories. Again, temporal effects (among-year climatic variation) appeared to exert more influence on these rates than spatial effects (among-territory differences in habitat composition and configuration). Although Lavier (2006) noted that this might be due to low variation in habitat composition and configuration among owl territories, amounts and arrangement of habitat features did influence the probability of colonization of temporarily vacant territories. Amount of interior forest and the density of interior forest patches positively influenced site colonization, whereas amount of meadow negatively influenced site colonization. No habitat features were identified as strongly related to site extinction probabilities.

Generally similar patterns were observed in studies on the other two subspecies of spotted owls. In most populations studied, differences in habitat composition and configuration among owl territories explained less of the variation in owl vital rates among these territories than did weather (Franklin and others 2000, Olson and others 2004, Blakesley and others 2005, Dugger and others 2005). In at least some cases, aspects of within-territory habitat configuration that were optimal for survival were suboptimal for reproduction (Franklin and others 2000).

All of the studies discussed above evaluated the effects of differences in habitat on vital rates among occupied owl territories. Therefore, these studies focused on areas that owls had already selected as home ranges. These areas presumably represent high-quality spotted owl habitat, and there is far less variability in habitat among these territories than between these territories and randomly available areas on the landscape (see **HABITAT USE AND SELECTION**, *Landscape Scale*).

Consequently, these studies should not be interpreted to mean that habitat exerts little or no influence on vital rates. Rather, they suggest that temporal variation in climate is more variable than spatial variation in habitat among occupied owl territories, and that climate therefore is an important driver of vital rates *within occupied owl habitat*. The amount and arrangement of suitable habitat likely drives patterns of owl distribution (UDSI FWS 1995: 83).

Life History Strategy

Available evidence suggests that the life history strategy of the Mexican spotted owl is generally similar to those of the better-known northern and California subspecies. These owls are characterized by high and reasonably constant adult survival rates, low juvenile survival rates, and relatively low and highly variable reproductive rates (for example, Noon and others 1992, Franklin and others 2000, 2004, Blakesley and others 2001, 2010, LaHaye and others 2004, Anthony and others 2006). This life history strategy allows owls to reproduce when conditions are favorable and to survive unfavorable periods with little or no reproduction.

The Mexican spotted owl differs from the other subspecies in other important respects. In northern and California spotted owls, the population appears to contain numbers of non-territorial “floaters” (Franklin 2001; Franklin and others 2000, 2004). These floaters fill vacancies in the territorial population, so that the territorial population remains relatively stable even during periods with little or no reproduction. In contrast, available evidence suggests that few such floaters exist in populations of Mexican spotted owls. Specifically, vacated territories may remain empty for years, and when territory vacancies are filled they are generally filled by subadult rather than older owls, suggesting that there is not a population of surplus owls unable to find vacant territories. As a result, population trend tracks changes in reproduction with a short time lag (Seamans and others 1999). Because reproduction in this owl is inherently variable, we can thus expect to see large variability in owl populations over time. Much of this temporal variability likely relates to large-scale climatic patterns (for example, Seamans and others 2002), which also are inherently variable within the range of the Mexican spotted owl.

Mortality Factors

Several mortality factors have been identified as potentially important with respect to the Mexican spotted owl, but we know little about the extent or relative importance of factors that cause mortality. Most owls that die are never found, and cause of death often is difficult to determine even for owls that are found.

Most known mortality of territorial adult and subadult owls occurred from November through February (Ganey and Block 2005a), suggesting that most mortality occurs during the winter months for territorial owls. In contrast, mortality of juvenile owls was observed even before they left their natal areas (late September through October). Juvenile mortality rates were high during the early dispersal period (October and November), and mortality was observed throughout the year (Ganey and others 1998, see also Willey and van Riper 2000).

Several potentially important causes of mortality are discussed below. Some of these factors can influence owl populations by impacting reproduction in spotted owls as well as by causing mortality. To reproduce, individuals must survive to a breeding period and have sufficient energy resources to produce and rear offspring. Thus, owl abundance can be influenced not only by factors determining the number of owls surviving to breed, but also by factors determining how many of those owls obtain sufficient energetic resources to allow breeding.

Predation—Predation may be a common mortality factor of spotted owls, accounting for at least five of 10 deaths documented among radio-marked adult and subadult Mexican spotted owls and 14 of 29 documented mortalities of radio-marked juveniles (Table 15; fig. 21). The specific predator is typically unknown, but may include procyonid mammals and especially avian predators

Table 15. Known causes of mortality of radio-marked Mexican spotted owls.

Age-class	Recovery unit ¹	N ²	Mortality cause			Source ⁵
			Predation	Starvation ³	Unknown ⁴	
≥2-yr-olds	UGM	21	1	2	2	1
≥2-yr-olds	BRE	13	4	1	0	2
≥2-yr-olds	Both RUs	34	5	3	2	1, 2
<1-yr-olds	UGM	24	5	4	0	3
<1-yr-olds	CP	31	9	11	0	4
<1-yr-olds	Both RUs	55	14	15	0	3, 4

¹ Recovery Units: UGM = Upper Gila Mountains, BRE = Basin and Range-East, CP = Colorado Plateau.

² Number of radio-marked owls.

³ Includes owls with cause of death listed as exposure in Willey and van Riper (2000: Table 1).

⁴ Indicates owl was found dead, but cause of death could not be determined.

⁵ Source: 1 = Ganey and Balda (1989a), Ganey and others (1999); 2 = Ganey and others (2005); 3 = Ganey and others (1998: Table 1); 4 = Willey and van Riper (2000: Table 1).



Figure 21. Remains of a color-banded Mexican spotted owl. Suspected cause of death was avian predation. Again, note numbered metal band (right leg) and color band (left leg). The specific predator could not be identified, although the remains were found in an area occupied by a resident pair of goshawks, suggesting possible predation by a goshawk.

such as great horned owls and northern goshawks. Some of these predators occupy the same general habitats as the spotted owl and are suspected to prey on spotted owls, although direct evidence of such predation is sparse (Gutiérrez and others 1995). Results from radio-marked Mexican spotted owls indicate that all age classes are preyed upon (Ganey and others 1989b, 1998, 2005, see also Willey and van Riper 2000).

Starvation—Starvation may be another common source of mortality (Table 15). Starvation accounted for 15 of 29 documented deaths of radio-marked juveniles, and occurred throughout the dispersal period. In contrast, starvation has not been observed in many deaths of adult and subadult owls (Table 15) and generally occurred in mid-winter in adults and subadults (for example, Ganey and others 2005). Juvenile spotted owls may be more vulnerable to starvation than adults because of their poor hunting skills (Ganey and others 1998, Willey and van Riper 2000). Starvation also could result from low abundance or availability of prey, which could affect both adults and juveniles, and which is most likely to occur from late fall through winter when prey resources generally are reduced in abundance (Ward 2001, Block and others 2005: Figure 1). In addition, starvation may predispose young or even adults to predation (Ganey and others 2005). When starvation occurs in resident adults due to low prey populations that are regionally synchronous, this form of mortality can influence a number of owls at one time. When low survival is combined with lack of reproduction, which also could occur when prey populations are low, population decrease can be rapid. This pattern has been observed in some Mexican spotted owl populations (Seamans and others 1999, Ward 2001).

Accidents—Accidents may be another mortality factor. For example, there are documented cases of spotted owls being hit by cars (USDI FWS 1995) and one documented case of electrocution (Gutiérrez and others 1996). The type of roads at which mortalities of spotted owls occurred ranged from unpaved forest roads to paved highways. Owls flying at night also might collide with power lines, tree branches, or other obstacles. This might be particularly true for birds migrating or dispersing through unfamiliar terrain (Martin 1986). Little information is available either on how frequently this might occur, or when it occurs. Again, starvation or at least hunger could predispose owls to accidents if it drives them to hunt along roadsides, in unfamiliar areas, or in weakened condition.

Disease and Parasites—Little is known about how disease and parasites affect Mexican spotted owls. One disease of particular concern to birds is West Nile Virus (WNV). This virus was first identified in Africa, and was detected first in the United States in 1999, in New York (McLean 2006). It spread rapidly across the country and has now reached the range of the Mexican spotted owl. Avian mortality from WNV has been extensive in North America (>48,000 dead birds reported from >200 species, McLean 2006). Owls appear to be fairly susceptible, with reported mortality rates of 43 and 97% from two studies in Canada ($n = 235$

and 73 captive owls, respectively), and at least 17 species testing positive for WNV (Mclean 2006: Table 4). We are unaware of any incidence of WNV in Mexican spotted owls, or of any program (systematic or otherwise) of surveillance for this disease in the subspecies. Thus, all we can say with certainty at this time is that WNV has arrived, and it has the potential to significantly impact population viability of Mexican spotted owls.

Relative to parasites, Hunter and others (1994) found hippoboscid fly larvae in the ears of 6 of 18 live Mexican spotted owls examined. They suggested that larval infestations in their ears could affect the owls' hearing. Because hearing is important for foraging at night, such infestations could eventually affect the birds' ability to hunt effectively. Hippoboscid flies also serve as vectors for several hematazoan (blood-borne) parasites in birds (Young and others 1993), and infection rates of such blood-borne parasites appear to be high in spotted owls. Gutiérrez (1989) found an infection rate of 100 percent in a survey of blood parasites in all three subspecies of spotted owls. A recent survey in northern and California spotted owls found infection rates of 52 and 79% respectively, and many owls harbored multi-species infections (Ishak and others 2008).

The effects of both parasites and disease likely vary depending on the condition of individual owls, with infections that are normally nonpathogenic assuming greater importance in owls that are stressed or malnourished (Young and others 1993). Therefore, both disease and parasites can interact with other factors such as climate and prey availability, and these interactions likely determine the ultimate effect of disease and parasite infections.

Prey Ecology

Although the strong link between raptors and their food is well documented (Newton 1979), few studies have quantified the relationships among spotted owls, their prey, and the environmental factors that influence the availability of favored prey to this owl (Ward 2001, Noon and Franklin 2002). Understanding a predator's food choices along with the natural and life history of its common prey species can provide practical information for conserving and enhancing the predator's habitat.

Hunting Behavior

Mexican spotted owls typically locate prey from an elevated perch by sight or sound, then pounce on the prey and capture it with their talons (Ganey 1998; fig. 22). They also have been observed capturing flying prey such as bats, birds, and insects (Duncan and Sidner 1990). They hunt primarily at night, although infrequent diurnal foraging has been documented, especially by pairs that had young to feed (Delaney and others 1999a). Owls in this study delivered 10 times as much food to nests during nocturnal hours as during daytime hours (0.37 versus 0.03 prey items hr^{-1} , respectively [Delaney and others 1999a: 44]).



Figure 22. Mexican spotted owl attacking a mouse on a branch (top; mouse provided by RMRS crew members in an effort to assess owl pair and reproductive status), and pouncing on prey on the ground (bottom). Photos: Darrell L. Apprill.

Mexican Spotted Owl Diet Composition

Several studies provided information on diets of Mexican spotted owls within the UGM RU based on examination of prey remains from regurgitated owl pellets (fig. 23). Although this is an accepted method for estimating diet composition of raptors and especially owls (Marti 1987), it may be subject to unknown biases. For example, the opportunistic nature of pellet sampling may result in a sample that is not fully representative of the overall diet. Many of these studies obtained large samples of prey items, which somewhat alleviates concerns about sampling error. In addition, however, soft-bodied prey (for example, insects such as butterflies and moths; Lepidoptera) may be under represented in pellets.



Figure 23. Regurgitated owl pellets (top). Diet composition can be estimated based on skeletal remains (middle) or other prey remains (such as pieces of beetle exoskeletons, bottom) found within these pellets. Photos: Todd A. Rawlinson.

Owls in all areas studied consumed a wide range of prey, including small terrestrial mammals, bats, birds, and insects (Table 16; see also Ward and Block 1995, Tables 5.2 and 5.5). Although diet composition varied among study areas, mammals dominated the diet, comprising >85% of estimated prey biomass in all study areas and >90% of prey biomass in five of six study areas. A few groups of small mammals dominated the diet in all study areas. These groups included woodrats, white-footed mice, voles, cottontail rabbits, and Botta's pocket gophers. Collectively, these five prey groups comprised >65% of prey biomass in all study areas, and >85% of prey biomass in all but one study area (Table 16, fig. 24). Thus, owls in all areas tended to specialize on a few types of small mammals, most of which were active at night. Diurnally active mammals such as squirrels and chipmunks (Sciuridae) typically were eaten in fairly small numbers. Most woodrats consumed were Mexican woodrats.

Table 16. Diet composition of Mexican spotted owls in various study areas, Upper Gila Mountains Recovery Unit, Arizona and New Mexico. First column within study area shows percent of total prey numbers¹, second column shows percent of estimated prey biomass.

Prey type	Study area ²											
	Walnut Canyon		SF Peaks		White Mountains		Coconino NF		Gila NF		Bar-M Canyon	
	No.	Biomass	No.	Biomass	No.	Biomass	No.	Biomass	No.	Biomass	No.	Biomass
Woodrats	33.1	50.0	18.5	49.1	17.8	36.6	12.4	43.2	19.0	50.5	7.8	27.8
White-footed mice	26.3	5.7	33.0	12.5	20.4	6.0	38.4	19.4	38.8	15.6	37.3	17.3
Voles	14.3	4.5	27.2	15.0	37.6	16.1	3.3	2.8	9.8	6.8	1.9	1.1
Rabbits	8.4	29.6	1.1	6.7	5.1	24.3	0.4	2.8	2.9	14.3	0.8	7.8
Pocket gophers	6.0	6.1	5.1	9.1	5.7	7.9	5.5	17.2	2.3	5.5	5.5	15.5
Bats	1.7	0.2	0.0	0.0	0.0	0.0	0.8	0.2	0.9	0.1	0.9	0.3
Other mammals	3.0	2.3	3.3	4.4	5.7	6.0	0.9	2.6	1.1	1.2	9.0	24.0
Birds	2.5	1.5	2.9	3.1	3.8	3.1	6.6	10.9	4.6	5.6	3.0	5.2
Insects	4.6	<0.1	9.1	<0.1	3.8	<0.1	31.7	0.9	20.6	0.4	33.7	0.9

¹ Sample sizes (number of prey items): Walnut Canyon = 711; SF (San Francisco) Peaks = 276; White Mountains = 157; Coconino National Forest = 1,631; Gila National Forest = 2,162; Bar-M Canyon = 1,125.

² Study areas are described in Appendix 2. Sources: Walnut Canyon, SF (San Francisco) Peaks, and White Mountains = Ganey (1992: Table 1); Coconino and Gila NFs (National Forests) = Seamans and Gutiérrez (1999: Table 1); Bar-M Canyon = Block and others (2005: Table 1). Ward and Block (1995) provided preliminary analyses for the Coconino National Forest, Gila National Forest, and Bar-M Canyon study areas. Numbers here differ from Ward and Block (1995) due to analysis of additional samples and/or use of updated, area-specific estimates of prey mass.

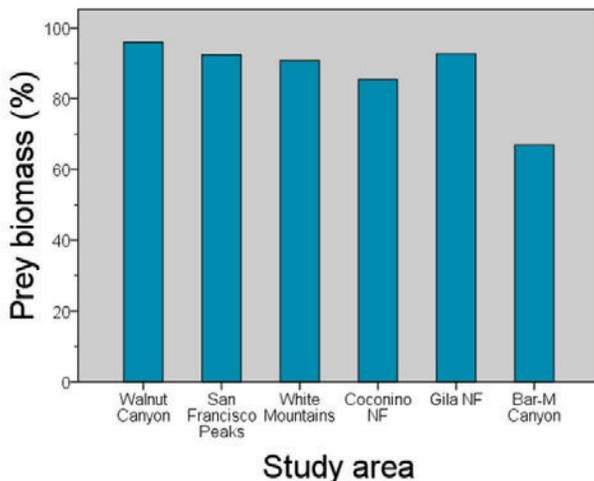


Figure 24. Proportion of prey biomass in the diet of Mexican spotted owls provided collectively by five groups of small mammals (woodrats, mice, voles, rabbits, and gophers). Data sources are described in Table 16 and study areas are described in Appendix 2.

Most white-footed mice consumed were deer mice, although considerable numbers of brush mice were consumed in some areas (for example, Seamans and Gutiérrez 1999, Block and others 2005). Most voles consumed were Mogollon voles, although long-tailed voles were eaten regularly in some study areas (for example, Seamans and Gutiérrez 1999).

Little is known about temporal variation in diets of Mexican spotted owls. Most prey remains used to estimate diet composition were collected during the breeding season, rendering seasonal comparisons impossible. Ganey (1992) reported variation among years in diet composition in two study areas in Arizona (Table 17). This likely reflects opportunistic foraging on variable prey resources, as several of the major prey species are known to fluctuate in abundance among years (fig. 25).

Table 17. Annual variation in diet composition (% of prey numbers) of Mexican spotted owls from two study areas within the Upper Gila Mountains Recovery Unit. From Ganey (1992: Table 2). *N* = number of prey items.

Study area ¹	Year	N	Prey type				
			Woodrats	W-f mice ²	Voles	Other mammals	Other
Walnut Canyon	1984	116	42.2	25.0	10.3	12.9	9.5
	1985	249	21.7	28.1	20.1	19.3	10.8
	1986	188	41.0	27.1	10.1	19.7	2.1
	1987	102	32.4	24.5	13.7	24.5	4.9
San Francisco Peaks	1986	61	18.0	24.6	16.4	18.0	23.0
	1987	110	10.0	56.4	23.6	6.4	3.6
	1988	79	25.3	10.1	44.3	7.6	12.7

¹ Study areas are described in Appendix 2.

² W-f mice = White-footed mice.

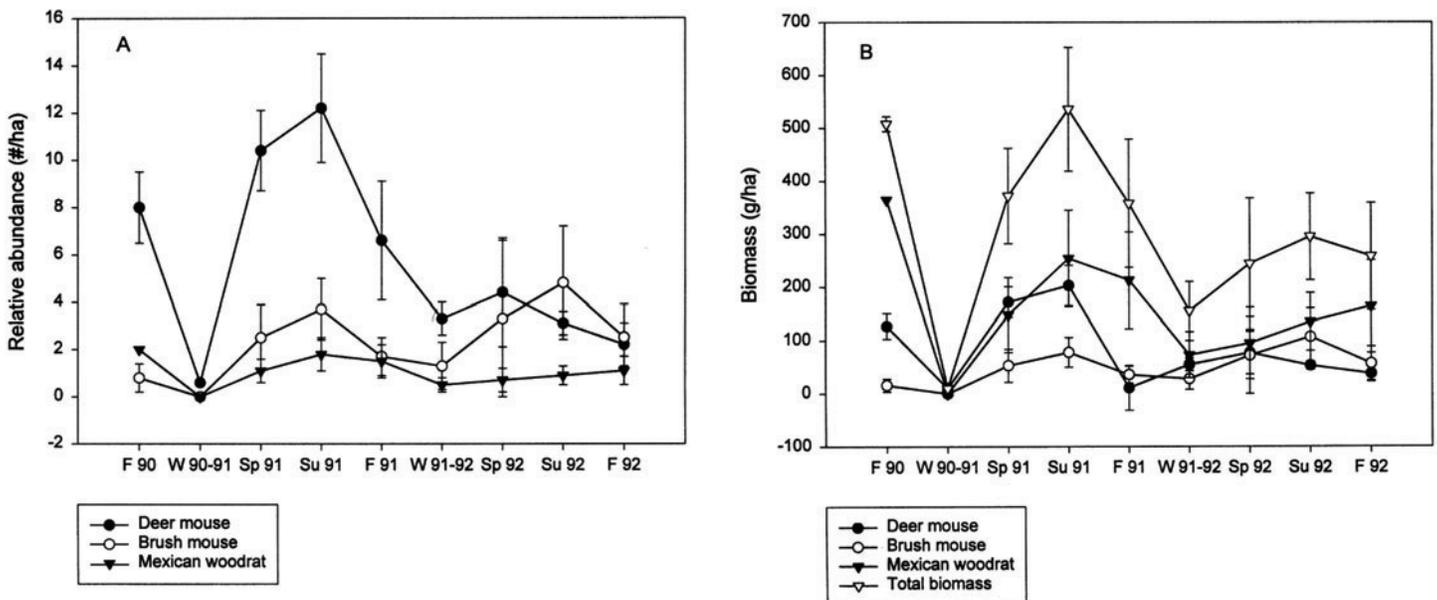


Figure 25. Seasonal and annual variation in abundance and biomass of some major prey species in the Bar-M Canyon study area, Arizona, based on live-trapping. Reprinted from Block and others (2005: Figure 1). Used by permission from The Wildlife Society.

Block and others (2005) compared diet composition of radio-marked Mexican spotted owls from four home ranges in pine-oak forest (Bar-M Canyon study area) with the relative abundance of major prey species within those home ranges as indexed by live-trapping. Owls at two of these sites ate more woodrats and fewer white-footed mice than expected based on indices of relative abundance, whereas owls at the other two sites consumed woodrats and white-footed mice as expected based on these indices. This may suggest that some level of prey selection is occurring, but it also could be an artifact of sampling variation. Specifically, the labor intensive nature of live-trapping efforts makes it very difficult to obtain accurate estimates of relative abundance of small mammals across the large home ranges used by foraging spotted owls.

Prey Abundance

Several studies have estimated prey abundance within ponderosa pine or ponderosa pine–Gambel oak forests within the UGM RU (Table 18; fig. 26). Estimates varied among studies, but abundance typically was both greater and more variable for deer mice than for most other species. In the only study that evaluated seasonal and annual variation (Block and others 2005), abundance varied among years,

Table 18. Density (range in number ac^{-1})¹ of selected small mammals in ponderosa pine and ponderosa pine–Gambel oak forest, Arizona.

Source	Deer mouse	Brush mouse	Mexican woodrat	Pocket gopher
Goodwin and Hungerford (1979)	2–19	6–20	2–10	<0.2
Block and others (2005: Figure 1)	1–5	0–2	0–0.4	
Kyle and Block (2000)	0.4–4.7			
Converse and others (2006)	2.2–12.6 ²		0–2.5	

¹ To convert densities to number ha^{-1} , multiply by 2.47. Estimates in Converse and others (2006) were model-based, other estimates were based on indices of minimum number alive.

² Estimate provided in Converse and others (2006) was for deer and brush mice combined.



Figure 26. A captured Mexican woodrat in a Sherman live trap. Live-trapping and mark-recapture analysis typically is used to estimate abundance of prey species. This woodrat is a recapture, as indicated by the presence of metal ear tags. These numbered ear tags are used to uniquely identify individual animals. Capture histories of these individuals across capture occasions are used to estimate abundance. Photo: Niki vonHedemann.

and within years abundance generally rose during spring, peaked during summer, and declined during fall and winter (fig. 25). Density of deer mice was the most variable, ranging from a high of 4.9 mice ac^{-1} (12.2 ha^{-1}) during summer 1991 to a low of 1.3 mice ac^{-1} (3.3 ha^{-1}) during winter 1991-92. Relative abundance of brush mice and woodrats generally was low in all seasons and years.

No information is available on densities of important prey species in mixed-conifer forests within the UGM. However, Ward (2001) provided data for several major owl prey species in four cover types in the Sacramento Mountains (Basin and Range-East RU), including mixed-conifer forest. Densities for all species varied among cover types (Table 19). Deer mice were relatively ubiquitous, occurring in all cover types. Brush mice were most abundant in xeric forest, occurred rarely in mixed-conifer forest, and were not captured in montane meadows. Both Mogollon (formerly Mexican) and long-tailed voles were most abundant in montane meadows, although mean densities of long-tailed voles also ranged from 1.3 to 2.6 ac^{-1} (3.3 to 6.4 ha^{-1}) in mixed-conifer forest (Ward 2001). Mean density of Mexican woodrats was greatest in xeric forest (Ward 2001), but they occurred in all habitats and the range in observed density was similar for xeric forest and mixed-conifer forest (Table 19). In general, densities for most species fell within ranges reported for ponderosa pine and pine-oak forests within the UGM RU (see Table 18).

Ward (2001: Table 2.9) also estimated biomass of these prey species during the summer within these cover types and evaluated variability in summer biomass across space (in other words, among cover types) and time (among years). Biomass of brush mice and woodrats differed significantly among cover types, whereas biomass of other species did not. Biomass of all species except the Mexican woodrat differed significantly across years, and the year effect was nearly significant for woodrats ($P = 0.059$). Cover type by year interactions were observed for brush mice and both vole species, indicating that population trends were not always synchronous in different cover types. Similar interactions were not observed for deer mice and woodrats.

Table 19. Range in summer density (number ac^{-1}) of selected small mammals in four cover types in the Sacramento Mountains, New Mexico (Basin and Range—East Recovery Unit), 1991-1996. Data from Ward (2001: Appendix 2.D).

Cover type ²	No. ³	Deer mouse	Brush mouse	Mogollon vole	Long-tailed vole	Mexican woodrat
Mesic forest-L	5	1.3-4.6	0-0.1	0-0.8	0.1-5.0	0-0.8
Mesic forest-M	23	0.4-24.7	0-2.1	0-5.3	0-13.7	0-1.3
Montane meadow	22	0.2-17.4	— ⁴	0-74.2	0-21.8	0-0.8
Xeric forest	25	0.1-4.9	0-9.4	0-5.0	0-0.2	0-1.3

¹ To convert densities to number ha^{-1} , multiply by 2.47.

² Cover types: Mesic forest = mixed-conifer forest (L = late-seral stage, M = mid-seral stage); Montane meadow = grassland; Xeric forest = ponderosa pine forest and pinyon-juniper-oak woodland.

³ Number of sites + years sampled.

⁴ No individuals ever captured in this cover type.

Prey Abundance and Owl Reproduction

Several studies have shown that successfully breeding northern and California spotted owls consume more large prey (for example, woodrats) than pairs that do not breed successfully (Barrows 1987, Thraillkill and Bias 1989, White 1996, Smith and others 1999). However, successfully breeding Mexican spotted owls in the UGM RU did not consume larger prey than non-breeding pairs (Seamans and Gutiérrez 1999). In general, reproduction and survival of Mexican spotted owls are more likely a function of total prey biomass consumed by these owls than of the biomass of any single prey species (Ward and Block 1995, Ward 2001).

Prey Habitat Relationships

Understanding habitat relationships of important prey species can provide additional information relative to foraging behavior and ecology of a predator and may provide valuable information for managers interested in maintaining or increasing prey populations. Several studies have provided information on habitat relationships of important prey species in ponderosa pine and ponderosa pine–Gambel oak forests within the UGM.

Kyle and Block (2000) sampled abundance of small mammals in two areas impacted by large wildland fires. Deer mouse densities one year post-fire were strongly correlated with percent cover of both forbs and shrubs (Kyle and Block 2000: Figures 3 and 4). Block and others (2005) reported that deer mice were relatively ubiquitous in their study area and that these mice occupied areas with variable conditions. They tended to occur most commonly in forests with sparse woody vegetation cover from 3-16 ft (1-5 m) aboveground and high stump density. Goodwin and Hungerford (1979) also noted a strong correlation between deer mouse abundance and amounts of woody debris, including stumps. Combined densities of deer and brush mice were negatively related to tree density in areas studied by Converse and others (2006).

Goodwin and Hungerford (1979) reported that both brush mice and woodrats were associated with rock ledges and slides, and that both species also used windrowed slash piles. Block and others (2005) found that brush mice were restricted to communities with a strong oak component and dry, rocky substrates with sparse tree cover, and Mexican woodrats typically occurred in areas with considerable shrub or understory tree cover, low grass cover, high volumes of large logs, and/or presence of rock outcrops. Converse and others (2006) also found that woodrat abundance was related to shrub cover and amounts of woody debris.

Using a different study design (occupancy monitoring modeled with habitat covariates across numerous sites), Kalies and Chambers (2010: Table 1) found that deer mice were positively associated with density of trees >20 in (50 cm) dbh and snags >16 in (40 cm) dbh, and negatively associated with down wood volume. Mexican woodrats were positively associated with pine basal area and slash, and negatively associated with an index of forest clumpiness. Mogollon voles were

positively associated with understory vegetation cover, clumpiness, and large snags, and negatively associated with pine basal area, oak basal area, density of trees >16 in (40 cm) dbh, and total snag density. Pocket gophers were positively associated with understory vegetation cover, understory species richness, clumpiness, and density of trees >24 in (61 cm) dbh, and negatively associated with snag density and down wood volume.

No similar information is available for mixed-conifer forests within the UGM RU, but Ward (2001) modeled relationships between habitat characteristics and biomass per unit area of small mammals in a study area that included mixed-conifer forest in the Sacramento Mountains, New Mexico (Basin and Range-East RU). Deer mouse abundance was positively related to mean maximum grass-forb height (Ward 2001: Table 2.23). Brush mouse abundance was positively related to percent rock cover, shrub density, and oak density. Abundance was positively related to mean maximum grass-forb height for both species of voles, and abundance of long-tailed voles was negatively related to shrub density. Abundance of Mexican woodrats was related to percent rock cover, shrub density, and density of logs >11.8 in (30 cm) in mid-point diameter, but the direction of the relationships were unclear and possibly non-linear (Ward 2001: Table 2.23).

Prey Diet Composition

Understanding diet composition of major prey species taken by Mexican spotted owls could provide insight into particular species or functional groups of plant species important to these species. This information in turn could provide insight for managers attempting to provide food resources for prey species. Unfortunately, only one study has estimated diet composition for small mammals in the UGM RU. That study (Goodwin and Hungerford 1979) evaluated summer diet composition (based on stomach samples) of several of the major prey species or groups taken by Mexican spotted owls in a study area that overlapped both the CNF and BMC study areas (Appendix 2). Diets of all species or groups were dominated by forbs and grasses, but some species also consumed considerable numbers of insects (Table 20). No information was provided on use of shrubs.

Table 20. Diet composition of selected small mammals in ponderosa pine and ponderosa pine–Gambel oak forest, Upper Gila Mountains Recovery Unit, as estimated from stomach contents. From Goodwin and Hungerford 1979: Figure 3.

Prey species	Diet composition (% of volume)				
	Forbs	Grasses	Trees	Insects	Unknown
Deer mouse	70	8	0	13	9
Brush mouse	61	11	0	12	15
Woodrats	49	16	0	20	15
Pocket gopher	46	38	3 ¹	3	10

¹ Indicates consumption of seedlings (Goodwin and Hungerford 1979: 10).

This may indicate either that shrubs were not eaten in significant amounts, or that they were lumped with forbs or included in the unknown group. Seed heads and flowers accounted for approximately 75% of the diet, with leaves and stems providing most of the other 25%. Only pocket gophers ate root material, and seedlings comprised about 3% of the pocket gopher diet. Goodwin and Hungerford (1979) noted that tree seeds and seedlings may be more important during fall and winter, when forbs and grasses are less abundant.

Effects of Disturbance on Small Mammal Populations

Habitat conditions for the owl's prey, access to those prey, and abundance of these prey species also can be changed by disturbance factors such as fire and forest treatments. Adequate long-term studies of small mammal populations have not been conducted to determine effects of these factors on many of the owl's prey species, but several studies have presented short-term results.

Kyle and Block (2000) estimated densities of two species of small mammals one year after two large wildland fires burned through ponderosa pine forest. Deer mouse densities generally were greatest in severely burned plots, intermediate in moderately burned plots, and lowest in unburned plots (Kyle and Block 2000: Figure 2). Gray-collared chipmunk density did not differ between unburned and moderately burned plots, but they were not captured on severely burned plots. Converse and others (2006) suggested that prescribed fire in dense ponderosa pine stands could benefit deer mice and Mexican woodrats by allowing increased shrub growth. They suggested that overly frequent prescribed fire could reduce small mammal abundance by reducing shrub density and amounts of woody debris, the habitat components most strongly related to small mammal abundance in their study.

Few studies have evaluated effects of forest harvest treatments on small mammals within the UGMRU. Goodwin and Hungerford (1979) concluded that clearcutting in ponderosa pine likely would eliminate gray-collared chipmunks and golden-mantled ground squirrels, and that thinning generally would benefit deer mice but could be detrimental to gray-collared chipmunks. They suggested that both brush mice and Mexican woodrats could benefit from slash retention, and that slash management exerted a stronger effect on mammal abundance and diversity than thinning itself.

Converse and others (2006) also concluded that thinning negatively affected gray-collared chipmunks but found no significant relationships between forest treatments and abundance of deer mice, Mexican woodrats, or golden-mantled ground squirrels. They also suggested that retaining slash after thinning treatments could benefit both woodrats and gray-collared chipmunks.

Kalies and Chambers (2010) modeled time since treatment (presumably most treatments involved tree thinning here) as a covariate to occupancy rate for eight species of small mammals. Four species showed a significant response, with Mexican woodrats responding positively to time since treatment and Mogollon

voles, rock squirrels, and gray-collared chipmunks responding negatively. That is, occupancy rates were lower for woodrats in areas where recent treatments had occurred, whereas occupancy rates of Mogollon voles, rock squirrels, and gray-collared chipmunks were greater in such areas.

Summary—Prey Ecology

Available data on spotted owl diet composition suggest that owls are opportunistic predators that eat a wide variety of prey but typically prey primarily on a relatively few groups of small mammals that are active at night. As noted earlier, significant relationships between consumption of large prey and successful breeding have not been observed in Mexican spotted owls, and efforts to link owl reproduction to consumption of particular prey species have been mostly unsuccessful. In fact, owl reproduction appears most linked to combined biomass of multiple prey species (for example, Ward 2001), as might be expected in an opportunistic predator.

Major prey species eaten by spotted owls differ in their habitat relationships and response to disturbance, although available data on these aspects of prey ecology are not entirely consistent across studies. Several studies suggest that retention of slash and coarse woody debris can be important and may mitigate otherwise negative impacts of forest treatments (Goodwin and Hungerford 1979, Block and others 2005, Converse and others 2006, Kalies and Chambers 2010, Block and others in press). Maintaining greater understory vegetation cover, height, and species richness should benefit several species, including voles and pocket gophers (Ward 2001, Kalies and Chambers 2010), and maintaining large (>16 in dbh [>40 cm]) snags and logs should benefit others, such as woodrats (Ward 2001, Block and others 2005, Kalies and Chambers 2010). Given the variation in habitat relationships across the small mammal community, a diversity of various habitat features across the landscape likely will best maintain high diversity, ensure maintenance of important ecological functions in that community (Kalies and Chambers 2010), and buffer against population fluctuations of individual prey species to provide a more constant food supply for the owl (Sureda and Morrison 1998, Ward 2001, Block and others 2005). An important consideration here is that many small mammals may respond to variation in habitat features at relatively fine scales and different species may respond to habitat features at different scales. Thus, these mammals may respond at variable scales that are generally smaller than those typically used in forest planning. Managers interested in managing prey habitat may need to adjust accordingly.

Interspecific Competition

In addition to other effects, forest management has the potential to affect competitive relationships among resident wildlife. Several other species of raptors and owls occur within the range of the Mexican spotted owl. Although raptors could compete with spotted owls for resources such as nest sites, they prey primarily on diurnally

active prey species. In contrast, most owls focus on the kinds of nocturnally active prey that dominate the diets of Mexican spotted owls. Thus, competition between owl species is suspected to be more important than competition between owls and raptors (for example, Marti and Kochert 1995). Logically, the species most likely to compete directly with Mexican spotted owls within the UGM RU is the great horned owl. This owl is sympatric with Mexican spotted owls throughout their geographic range, relatively similar in size within that geographic range, and both owls are active at night, suggesting that they could compete for nocturnally active prey (Gutiérrez and others 1995, Houston and others 1998). The great horned owl also may prey on spotted owls (Gutiérrez and others 1995).

Despite this potential for competition and possible predation by great horned owls on Mexican spotted owls, relatively little is known about interspecific interactions between the two. Ganey and others (1997) monitored sympatric, radio-marked spotted and great horned owls in Arizona (BMC study area). Home ranges were similar in size between these owls (Ganey and others 1997: Table 1) and overlapped considerably between species. On average, spotted owls shared at least $51.0 \pm 24.3\%$ (*SE*) of their breeding-season home range and $74.1 \pm 4.8\%$ of their non-breeding-season home range with great horned owls ($n = 6$ spotted owl and 3 great horned owl home ranges). The figures for proportions of great horned owl home ranges shared with spotted owls were similar (57.4 ± 12.2 and $70.5 \pm 12.3\%$ for breeding- and non-breeding-season home ranges, respectively; Ganey and others 1997: Table 2). These are minimum estimates of spatial overlap, because we cannot be certain that all owls in the area were radio-marked.

Home-range composition, in terms of four canopy-cover classes and three cover types, did not differ between species in either the breeding or non-breeding season (Ganey and others 1997: Table 4). In contrast, use of canopy-cover classes and cover types within the home range differed between species in at least some combinations of season and activity considered (Ganey and others 1997: Table 4). Differences typically were greatest with respect to roosting habitat used during the breeding season. For example, $>90\%$ of roosting locations for spotted owls during the breeding-season were in forests with canopy cover $>40\%$, whereas $>64\%$ of great horned owl roosting locations were in forests with canopy cover $<40\%$ (fig. 27; Ganey and other 1997: Table 5). Great horned owls also foraged primarily in forests with $<40\%$ canopy cover (78 and 71% of foraging locations during the breeding and non-breeding seasons, respectively). In contrast, $>50\%$ of spotted owl foraging locations occurred in forests with canopy cover $>40\%$ during both seasons (see fig. 27 for breeding season example). Spotted owls roosted primarily in ponderosa pine–Gambel oak forest during both seasons, sometimes roosted in ponderosa pine forest, and did not roost in meadow cover types (see fig. 28 for breeding season example; Ganey and others 1997: Table 6). In contrast, great horned owls frequently roosted in both pine-oak and ponderosa pine forest, and sometimes roosted in isolated clumps of trees within meadow cover types.

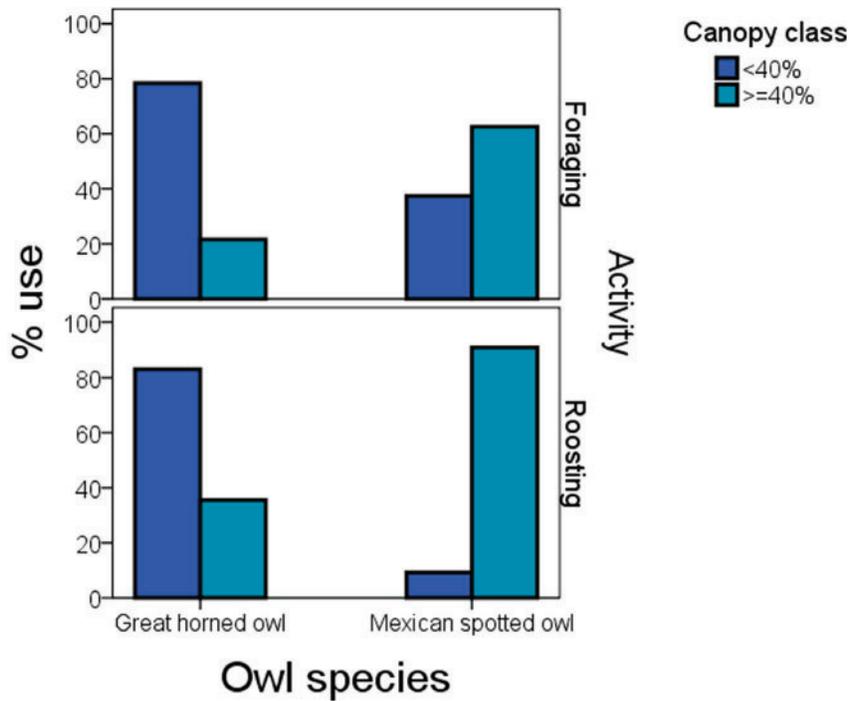


Figure 27. Use of two canopy-cover classes for foraging and roosting during the breeding season by radio-marked great horned and Mexican spotted owls, BMC study area, Upper Gila Mountains Recovery Unit. From Ganey and others (1997: Table 5).

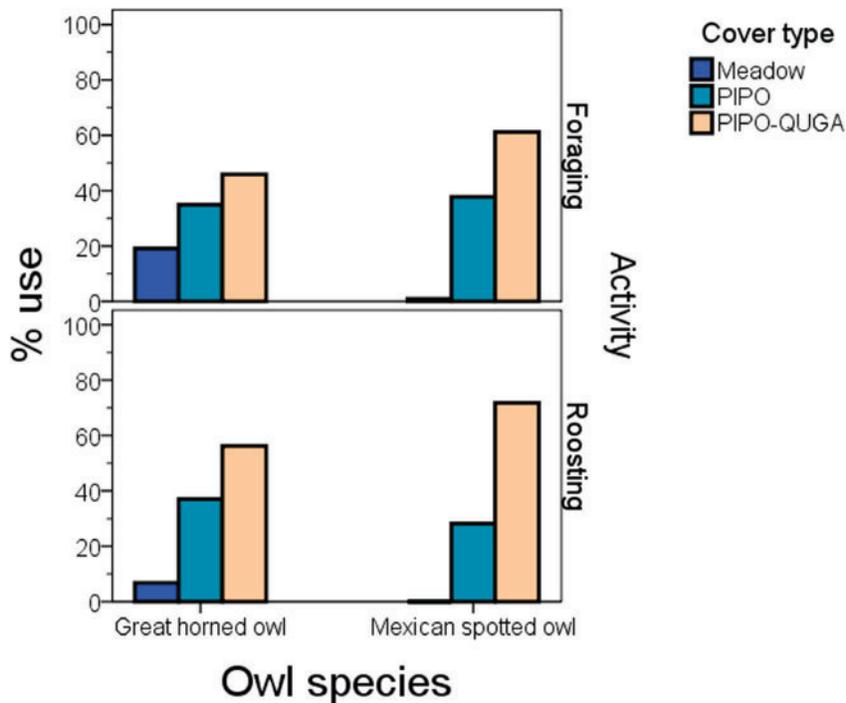


Figure 28. Use of three cover types for foraging and roosting during the breeding season by radio-marked great horned and Mexican spotted owls, BMC study area, Upper Gila Mountains Recovery Unit. From Ganey and others (1997: Table 6). PIPO = ponderosa pine forest, PIPO-QUGA = ponderosa pine–Gambel oak forest.

Both species of owls foraged in some of the same forest stands, but these stands were not necessarily used at the same time and spotted owls also foraged in many stands that great horned owls did not appear to forage in (Ganey and others 1997: Table 3). Stands used by foraging Mexican spotted owls had greater log volume and shrub cover than stands used by great horned owls in both the breeding and non-breeding seasons. During the non-breeding season, stands used by spotted owls also had greater canopy cover than stands used by great horned owls, and stands used by great horned owls had greater forb cover.

Nest stands and structures also appeared to differ between species, although sample sizes were very small. All spotted owls nested in ponderosa pine–Gambel oak forests, whereas sympatric great horned owls nested primarily in ponderosa pine forest. Nest stands used by spotted owls had significantly greater tree basal area, oak basal area, and canopy cover than nest stands used by great horned owls, and oak contributed a greater proportion of overall stand basal area in spotted owl nest stands (Table 21). As discussed earlier, Gambel oak basal area discussed here primarily refers to tree-form oak.

In terms of nest structures, all great horned owls nested either in stick nests built by other birds or in mistletoe broom platforms in ponderosa pine trees (Table 22). Stick nests were used uncommonly by Mexican spotted owls, and we have never observed a Mexican spotted owl nest in a mistletoe broom in ponderosa pine (although mistletoe brooms are commonly used in mixed-conifer forest; Table 14). Active nests of these species were sometimes located as little as 330 ft (100 m) apart, but in all such cases were in different stands (J. L. Ganey and W. M. Block, unpublished data).

These observations are consistent with the hypothesis that spotted owls may be avoiding competition with great horned owls (and potentially predation) by partitioning use of habitat resources over space and through time. Similar patterns have been observed for northern spotted owls living in sympatry with barred owls in conifer forests of Washington (Hamer and others 2007).

Table 21. Selected characteristics of nest stands used by sympatric, radio-marked great horned ($n = 5$ stands) and Mexican spotted owls ($n = 6$ stands) in a study area (Bar-M Canyon; Appendix 2) dominated by ponderosa pine and ponderosa pine–Gambel oak forest, Upper Gila Mountains Recovery Unit. Source: J. L. Ganey and W. M. Block, Rocky Mountain Research Station, unpublished data.

Parameter	Great horned owl		Mexican spotted owl	
	Mean	SE	Mean	SE
Live tree basal area ¹ (ft ² ac ⁻¹)	98.9	15.7	155.1	14.4
Gambel oak basal area ¹ (ft ² ac ⁻¹)	7.4	3.5	24.8	4.4
% Gambel oak basal area ²	7.5		16.0	
Canopy cover (%)	38.2	6.3	62.0	9.8

¹ To convert basal area to m² ha⁻¹, divide by 4.3554

² Percent of live tree basal area contributed by Gambel oak, calculated from above table values as: (Gambel oak basal area/Live tree basal area) * 100.

Table 22. Nest structures used (%) by sympatric, radio-marked great horned and Mexican spotted owls in a study area (Bar-M Canyon) dominated by ponderosa pine and pine–oak forest, Upper Gila Mountains Recovery Unit. Number of nests included in estimates in parentheses. Source: J. L. Ganey and W. M. Block, Rocky Mountain Research Station, unpublished data.

Nest structure	Great horned owl (5)	Mexican spotted owl (8)
Cavity	0.0	50.0
Stick nest (avian)	60.0	12.5
Squirrel nest ¹	0.0	37.5
Mistletoe broom ²	40.0	0.0

¹ Spotted owls flattened these structures and nested atop the resulting platform.

² All mistletoe brooms were in ponderosa pine trees.

Avoidance of competition by partitioning food was less apparent. Diet overlap was considerable between radio-marked Mexican spotted and great horned owls (Ganey and Block 2005b). Both species preyed primarily on nocturnally active small mammals, although both also ate birds and insects and great horned owls occasionally preyed on lizards. Mammals comprised 63 and 62% of the diets of spotted and great horned owls, respectively, based on total numbers of identified prey items in regurgitated pellets ($n = 1,125$ prey items for spotted owls and 94 prey items for great horned owls, respectively). In terms of prey biomass, mammals comprised 94 and 95% of the diets of spotted and great horned owls, respectively. Mean prey mass averaged 40.1 ± 1.8 g for spotted owls and 47.0 ± 7.4 g for great horned owls when all prey were included, and 60.0 ± 2.4 g and 69.7 ± 9.8 g, respectively, for all non-insect prey. Dietary overlap, calculated using Pianka's (1973) index, was 0.95. This index ranges from zero (no overlap) to 1 (complete overlap). Observed overlap in diet composition between species was greater than expected based on null models of diet overlap (Ganey and Block 2005b; null models generated using program ECOSIM; Gotelli and Entsminger 2001).

Thus, in this study area, home ranges of these species overlapped considerably. There also was overlap in areas used for foraging, as well as in the size and type of prey taken. This suggests a potential for both exploitation and interference competition for food resources, which are assumed to be limiting in some years (Verner and others 1992, Ward 2001). There also were strong differences in habitat-use patterns between species, however. These differences suggest that these species may be able to partition habitats in areas of sympatry, with spotted owls primarily using forests with canopy cover >40%, and great horned owls primarily using forests with canopy cover <40% (fig. 29).

Whether or not these patterns of habitat use are influenced by the presence of the other owl species is unknown. The observed habitat-use patterns for both species were generally consistent with known patterns from other studies (reviewed in Ganey and Dick 1995, Gutiérrez and others 1995, Houston and others 1998), as well as with morphological and behavioral characteristics of both species (Ganey and others 1997), suggesting that habitat use was not strongly influenced by the

presence of the potential competitor. However, we observed numerous instances of apparently agonistic calling encounters between radio-marked owls (J. L. Ganey, personal observation; see also Ganey 1990). This suggests that interference competition, where individuals physically interfere with each other, may occur, and may partially explain some of the apparent habitat partitioning observed. Regardless of the underlying mechanisms, at present these owls appear able to partition available forest habitats, and they likely take similar prey in different areas, minimizing direct competition for resources. This interaction could be altered if extensive forest management, wildland fire, or climate change reduces the area of forests with canopy cover >40%. This change could benefit the great horned owl and reduce habitat amount and/or quality for the spotted owl (Ganey and others 1997).

Human Disturbance

Although a variety of human-caused disturbances can affect birds of prey and other wildlife (Knight and Gutzwiller 1995), no published studies have evaluated the effects of human disturbance on spotted owls within the UGM RU. Delaney and others (1999b, Basin and Range-East RU) and Johnson and Reynolds (2002, Southern Rocky Mountains–Colorado RU) studied the response of Mexican spotted owls to overflights by helicopters and fixed-wing aircraft, respectively, in other Recovery Units. Both studies suggested that owls were fairly resilient to short-duration disturbance caused by overflights.

Delaney and others (1999b) also developed an owl-weighted frequency curve to simulate hearing sensitivity of owls in various parts of the sound-frequency spectrum and used this curve to evaluate relative disturbance levels caused by chain saws. Spotted owls were more sensitive to disturbance by chainsaws than by helicopter overflights at comparable distances, and most owls flushed from their perches when chainsaws were operated <197 ft (60 m) from roosts. Owl response decreased with increasing distance to noise source for both chainsaw operation and helicopter overflights, and Delaney and others (1999b) suggested that a buffer zone of 344 ft (105 m) would minimize impacts of helicopter overflights on spotted owls.

In a later study, Delaney and Grubb (2004) quantified relative, owl-weighted noise levels caused by road-maintenance equipment (rock crusher, loader, bulldozer/roller, and grader) in spotted owl habitat dominated by mixed-conifer forest (Basin and Range-East RU). They found consistent differences in noise levels between types of equipment, microphone positions (in trees versus on the ground), distance from noise source, and habitat (forest versus meadow). Rock crushers were louder than other equipment, sound levels were greater in trees than on the ground at all distances, sound levels decreased with distance, and sound levels were greater in meadows than in forests at comparable distances. They concluded that owls were capable of hearing all sound sources tested at distances of at least 1,312 ft (400 m). Owl response to these noise sources was not evaluated in this study.



Figure 29. An area contained with overlapping home ranges of radio-marked Mexican spotted and great horned owls, BMC study area, Upper Gila Mountains Recovery Unit. Great horned owls nested along the forest edge past the meadow shown in the foreground, and they frequently foraged from large trees and snags along this and similar forest edges, or in open stands (canopy cover <40%). Spotted owls nested on the forested butte shown behind the meadow and forest edge, and they roosted and foraged primarily in forests with >40% canopy cover. Also note that this photo provides an indication of the size of meadows discussed earlier in relation to this study area.

No studies have evaluated disturbance from recreational activities in the UGMRU. Swarthout and Steidl (2001, 2003) experimentally evaluated the effects of hikers on spotted owls in canyonlands terrain (Colorado Plateau RU). They quantified both flush responses and activity budgets of owls exposed to hikers. Owls exposed to hikers sometimes flushed from perches and spent more time vocalizing and less time handling prey and performing maintenance activities than owls not exposed to hikers. In general, owl response level was related to both perch height and distance to the hiker. Swarthout and Steidl (2003) concluded that cumulative disturbance caused by recreational hiking near nests likely would be detrimental only where owls occupied canyons receiving use by ≥ 50 hikers per day, and that placing a 180-ft (55-m) buffer zone around known owl roosting sites would eliminate most flush responses. A buffer of this size also would restrict hiker access to 80% of the narrow canyons occupied by Mexican spotted owls in their study area. They estimated that a 39-ft (12-m) buffer zone likely would minimize flush response while excluding access to only 25% of canyons occupied by owls.

In summary, the limited information available suggests that: owls may be disturbed by a variety of human-caused activities, ground-based activities generally are more disturbing than overflights, and decibel levels within the owl's hearing range and

distance to the source of disturbance are significant factors in determining owl response. No studies have evaluated potential effects of chronic disturbance on parameters such as site occupancy, nest-site selection, or demography of Mexican spotted owls. It is possible that even low levels of chronic disturbance may affect spotted owls in unknown ways.

Movements and Migration

The ability of Mexican spotted owls to move within and among habitats or across a landscape is a key factor for maintaining function and viability of populations over time. For example, small populations often require recruitment from larger (core) populations to persist for long periods, and movement across the landscape facilitates gene flow and the maintenance of genetic diversity. Understanding how frequently and under what conditions owls are successful in completing movements can allow better predictions about long-term or local viability. Knowledge for mobile organisms like spotted owls is often difficult to obtain, and details about conditions that allow for successful dispersal or explanations for periodic migration are limited. Nonetheless, a few studies have documented movements of this owl. This section summarizes existing knowledge about seasonal migration and dispersal movements of this owl and the processes that influence those movements.

Seasonal Migration

Ganey and Block (2005a) summarized available information on seasonal movements and range use of radio-marked Mexican spotted owls. They defined all radio-marked owls that moved >1.25 mi (2 km) from their breeding-season home-range center as “migrants,” and treated all other radio-marked owls as “residents,” with this distance criterion based on mean nearest-neighbor distances reported in studies of Mexican spotted owls in Arizona and New Mexico. Seasonal movements or migration occurred in all areas where movements of radio-marked owls were monitored within the UGM RU (Table 23). Seasonal migration generally involved a subset of the population, with the size of that subset varying both among study areas and among years within study areas.

Table 23. Numbers of radio-marked Mexican spotted owls observed to migrate during the winter in various studies within the Upper Gila Mountains Recovery Unit. From Ganey and Block 2005a: Table 2.

Study area ¹	Years	Number of radio-marked owls	Number of owls migrating ²
San Francisco Peaks	1986-1987	4	2
Walnut Canyon	1986-1987	2	2
Bar-M Canyon	1990-1993	13	3

¹ Study areas are described in Appendix 2.

² Migration was defined as movement > 1.25 mi (2 km) from the center of the breeding-season home range.

Migrating owls typically left study areas in November or December and returned from January to April (Table 24). Distance moved ranged from 3 to 31 mi (5 to 50 km) for owls whose wintering areas were located. Wintering areas of two owls from the San Francisco Peaks could not be located despite an aerial search covering thousands of square miles, suggesting that some owls may move long distances (see also Gutiérrez and others 1996).

Some radio-marked owls moved only short distances and remained in the same forest types represented in their breeding-season home ranges (Table 24). In contrast, other owls moved down in elevation, and most of these down-slope migrants wintered in habitats more open in structure than typical breeding habitat, such as pinyon-juniper woodland (Table 24). We also are aware of numerous anecdotal observations of Mexican spotted owls in woodland, semi-desert, and desert cover types during the winter months. In most cases, it is impossible to tell whether these represent migrating territorial owls or dispersing juveniles, which use similar habitats (Arsenault and others 1997, Ganey and others 1998, Willey and van Riper 2000, Duncan and Speich 2002).

Thus, available information suggests that seasonal migration of some individuals occurs in many or most populations of Mexican spotted owls, and that such migration occurs in both sexes (Tables 23, 24). Partial migration also occurs in California spotted owls (Laymon 1989, Verner and others 1992). In contrast, migration appears to be rare in northern spotted owls (Gutiérrez and others 1995).

Reasons why only some owls migrate are unknown. In addition, some individual Mexican spotted owls migrate in some years but not others (Table 24). Migration generally entails a change in elevation for both Mexican and California spotted owls (Laymon 1989, Verner and others 1992), with most owls moving down slope

Table 24. Distance moved, movement duration, elevation change, and habitats used by migrating adult or subadult Mexican spotted owls within the Upper Gila Mountains Recovery Unit. From Ganey and Block (2005a: Table 3). Study areas are described in Appendix 2.

Study area	Years	Sex	Distance moved (mi) ¹	Duration	Elevation change (ft) ²	Cover type ³
San Francisco Peaks	1986-87	F	Unknown ²	Nov-Apr	Unknown ⁴	Unknown
San Francisco Peaks	1986-87	M	Unknown ²	Nov-Apr	Unknown ⁴	Unknown
Walnut Canyon	1986-87	F	6.2	Dec-Jan	- 100	MC, PP, P/O/J, R
Walnut Canyon	1986-87	M	6.2	Dec-Jan	- 100	MC, PP, P/O/J, R
Bar-M Canyon	1990-91	M	6.2	Dec-Jan	0	PO
Bar-M Canyon	1990-91	M	31.1	Dec-Apr	- 920	PJW
Bar-M Canyon ⁵	1991-92	F	31.1	Dec-Apr	- 920	PJW
Bar-M Canyon ⁵	1992-93	F	31.1	Dec-Apr	- 920	PJW

¹ To convert mi to km, multiply by 1.609.

² To convert ft to m, divide by 3.28.

³ Cover types used during migratory period: MC = mixed-conifer forest, PJW = pinyon-juniper woodland, PO = ponderosa pine-Gambel oak forest, PP = ponderosa pine forest, P/O/J = ponderosa pine/oak/juniper, R = riparian. Cover types are described further in Appendix 3.

⁴ Wintering areas not located despite an aerial search covering thousands of square miles.

⁵ These two records represent one female owl that migrated to the same area in two consecutive winters. This owl did not migrate in the winter of 1990-1991 (but her mate did).

(but see Willey 1998a). Migration to lower elevations likely allows owls to winter in areas that are warmer during the winter than their breeding areas and that lack persistent snow. This may facilitate an energetic savings in maintaining homeostasis and hunting for small mammals, which comprise the bulk of the diet. It also may allow the owls to move to areas with more concentrated prey resources, as populations of small mammals reach their nadir in owl breeding areas during the winter months (Ward and Block 1995, Ward 2001, Block and others 2005). For example, Block and others (2005: 625) used live trapping to estimate available prey biomass during the winter both in the traditional breeding area and a wintering area used by a pair of radio-marked Mexican spotted owls (represented by the last three records in Table 24). Estimated prey biomass was almost eight times greater within the winter range than within the breeding area (486 g ac⁻¹ vs. 63 g ac⁻¹ [1,200 g ha⁻¹ vs. 155 g ha⁻¹]). Although circumstantial, the evidence suggests that migration may be triggered by reduced availability of food.

Also presently unknown is how and why migrating owls select particular wintering areas, as we have little information on specific habitat features that migrating Mexican spotted owls use in wintering areas. From a conservation perspective, some migrating owls occupy cover types that have no protected status under USDI FWS (1995). These cover types also are used by dispersing juvenile owls during the fall and winter (Arsenault and others 1997, Ganey and others 1998, Willey and van Riper 2000). The types of lowland areas in which wintering owls have been observed cover vast areas, and we have no evidence that suitable wintering areas are limiting. Thus, there is little evidence that specific protective measures for wintering areas or habitats used by migrating spotted owls are necessary at this time. Further, owls use these areas at a time of year when they are unlikely to vocalize (Ganey 1990), making it difficult to locate such areas through calling surveys. Lacking an effective way to identify important wintering areas limits our ability to implement conservation measures in such areas.

Dispersal

Two forms of dispersal occur in spotted owls. Natal dispersal, or dispersal by young of the year from their birth sites, is the most common form and begins each fall following the production of young. Breeding dispersal, or movement by subadult or adult owls from a previously occupied territory to another territory, occurs less frequently (Gutiérrez and others 1995, Forsman and others 2002, Blakesley and others 2006).

Natal Dispersal—Little information is available on natal dispersal by Mexican spotted owls within the UGM RU. Therefore, we have included information from other Recovery Units in the following discussion, as well as information from other subspecies of spotted owls, to supplement the available information from the UGM RU.

Natal dispersal by juvenile Mexican spotted owls has been studied directly by monitoring movements of radio-marked individuals (Arsenault and others 1997, Ganey and others 1998, Willey and van Riper 2000) and indirectly by monitoring movements of color-banded juvenile owls (Seamans and others 1999, Duncan and Speich 2002).

Radio-marked juvenile Mexican spotted owls began dispersing in September and October in all study areas, with most dispersing in September. Initial dispersal movements were rapid, abrupt, and random with respect to direction. Two types of behavior during natal dispersal followed initial movements: rapid dispersal across the landscape and extensive local exploration. Many dispersing juveniles exhibited periods of both types of movements. Distance from the natal site to the last observed location for radio-marked juveniles ranged from <1 to >57 mi (92 km; Ganey and others 1998: Table 1, Willey and van Riper 2000: Table 1). These distances likely represent minimum estimates of dispersal capability, as only one radio-marked juvenile was tracked until it settled on a territory and paired with a mate. Directions from natal sites to final observed locations did not differ from random, indicating that dispersing owls did not follow a singular path or corridor. In addition, dispersing juveniles used a wide variety of habitats, including some that were very different in structure and composition from typical breeding habitat.

Because juvenile survival typically is low (Table 14), documenting final dispersal distances using radio-marked birds requires following large numbers (>100) of radio-marked young for a longer (>3 years) period than most radio-transmitter batteries or funding for aerial monitoring will last (Forsman and others 2002). Similarly, results may be sparse in color-banding studies. Consequently, few estimates of natal dispersal distance are available for Mexican spotted owls that disperse successfully and subsequently establish a territory. Within the UGM RU, the single successful dispersal event observed among radio-marked owls involved an owl that traveled only 3.7 mi (6 km; Ganey and others 1998). Duncan and Speich (2002) documented four instances of successful dispersal among color-banded Mexican spotted owls in southern Arizona (Basin and Range–West RU). These owls crossed desert valleys between sky-island mountain ranges in southeastern Arizona, and distance between natal sites and territories established ranged from 17 to 34 mi (28 to 54 km).

It is not clear when natal dispersal typically ceases in Mexican spotted owls. La-Haye and others (2001) noted that >50% of successful natal dispersers in their California study area occupied territories within one year, and that virtually all successful dispersers occupied territories within three years. Forsman and others (2002) noted variable patterns in northern spotted owls, with some owls settling permanently in their second summer while others did not settle permanently until they were 2 to 5 yrs old. Thus, available evidence from other subspecies suggests that most young occupy territories in the first three years following fledging but that dispersal movements may continue for up to five years for some owls.

Breeding dispersal—Reasons for and distances traveled during dispersal by previously settled subadult and adult Mexican spotted owls are poorly understood. Breeding dispersal is thought to occur when a mate is lost, or in some cases when a better reproductive opportunity is found elsewhere. Examples of both have been documented for all three subspecies (LaHaye and others 2001, Forsman and others 2002, J. L. Ganey and J. P. Ward, unpublished data).

Arsenault and others (1997) noted apparent cases of dispersal in subadult Mexican spotted owls, and Gutiérrez and others (1996) suggested that dispersal also may occur in adult Mexican spotted owls. In both cases, the movements described could indicate seasonal migration rather than breeding dispersal. Forsman and others (2002) noted that breeding dispersal of northern spotted owls in Oregon and Washington occurred relatively infrequently. Based on settlement patterns of banded birds, distance dispersed ranged from <1 to 53 mi (<1 to 85 km) between previously and newly occupied breeding sites for all age classes. First-year subadults ($n = 71$) moved farther than second-year subadults ($n = 75$) and adults ($n = 294$ owls; median distances = 3.2, 2.6, and 2.0 mi [5.1, 4.1, and 3.5 km], respectively). Most (83%) adults that did disperse moved only once. Of those that moved more than once, 41% moved back to an original territory (Forsman and others 2002). There were no significant differences in breeding dispersal distances among the sexes, but the odds that an individual would move were generally greater for females and were greatly magnified for either sex if the pair bond was disrupted by disappearance (movement or death) of a mate.

In summary, juvenile dispersal appears to be obligate in Mexican spotted owls, and settled subadult or adult birds may on a much rarer basis move to another site. Juvenile owls leave the natal territory in September or October and wander the landscape. Many perish in the process. They are capable of moving long distances, but many successful dispersers occupy territories near their birthplace. Natal dispersers move through a wide variety of habitats during the dispersal period, many of which differ greatly from typical breeding habitat and have no formal protective measures under USDI FWS (1995; Ganey and Block 2005a). There is little existing evidence that would allow us to identify common dispersal directions, movement corridors, or important areas or habitats. Many Mexican spotted owls appear to occupy territories at 1 to 2 yrs of age, while others may settle when older. Some of this variation may be driven by trends in owl density and fecundity, manifested through trends in numbers of territory vacancies. In general, we know little about dispersal behavior, and especially about dispersal movements of Mexican spotted owls during and following their second summer of life.

Metapopulation Ecology

The structure and spatial distribution of spotted owls at a range-wide scale suggests that groupings of individuals may occur as subpopulations, and that these subdivided populations may function as a metapopulation (for example, Levins 1970,

Hanski 1998), or a series of subdivided populations where population interactions are much higher within than between populations (Gutiérrez and Harrison 1996; see also Shaffer 1985, Noon and McKelvey 1992, 1996, LaHaye and others 1994). Of the three subspecies, the distribution of Mexican spotted owls appears to most naturally resemble the metapopulation construct, with perceived subpopulations existing in useable habitat created by elevation gradients and disconnected mountain or canyon systems separated by a matrix of low-quality to non-useable habitat.

Landscape Connectivity

Despite the important contributions made by metapopulation theory and models to management of northern and California spotted owls (Shaffer 1985, Noon and McKelvey 1992, 1996, LaHaye and others 1994, Gutiérrez and Harrison 1996), few studies have examined metapopulation structure of Mexican spotted owls. Keitt and others (1995, 1997) examined the spatial pattern of forest habitat patches across the range of the Mexican spotted owl. Patches of forest habitat in the range of the Mexican spotted owl showed a connectivity threshold of approximately 28 mi (45 km), and the authors concluded that an organism capable of dispersing ≥ 28 mi (45 km) through inhospitable terrain, and with an average exponential dispersal distance of ≥ 9 mi (15 km), would perceive the landscape as a series of connected patches. They further concluded that Mexican spotted owls likely met these criteria, and that the Mexican spotted owl probably behaves as a classical metapopulation over much of its range. That is, habitat connectivity is such that many habitats are “nearly connected” at distances corresponding to the best empirical estimates of the owl’s dispersal capability. At this scale, the landscape consists of a set of large, more-or-less discrete habitat clusters. For example, most of the Mogollon Rim functions as a single cluster, the Southern Rocky Mountains as another single cluster, and so on. This suggests that owls could successfully disperse within habitat clusters with very high probability and disperse between clusters with much lower probability. Thus, we would expect owls to disperse within clusters most of the time and between clusters rarely, which is consistent with the definition of a metapopulation. Maintaining or increasing habitat connectivity across the owl’s range thus could facilitate owl movements, provide opportunities for local population failures to be “rescued” by immigration from other populations, and facilitate gene flow among populations (Barrowclough and others 2006).

Positional Effects on Landscape Connectivity

Keitt and others (1995, 1997) also attempted to identify the habitat clusters most important to overall landscape connectivity, using maps based on forest and woodland cover to define habitat clusters. They first ranked habitats to emphasize the importance of large patches in the landscape. The UGM RU emerged as most important overall in this analysis, because of its large area and relatively continuous forest habitat. They next conducted a second analysis aimed at emphasizing positional effects on landscape connectivity. The UGM RU again emerged as important in this analysis, due to both its large size and central location. But some small habitat clusters also emerged as important. Because of their locations, these

clusters may serve as stepping stones between other, larger clusters and thus may be important to landscape connectivity despite supporting relatively few resident owls. Conclusions about the importance of specific habitat clusters depend heavily on the accuracy of the underlying map of habitat clusters, which remains unknown.

Patch Occupancy

Urban and Keitt (2001) used a graph-theoretic perspective to evaluate the effects of habitat loss on patch occupancy by Mexican spotted owls. They assumed that the Mexican spotted owl population functioned as a metapopulation and used Hanski's incidence function (Hanski 1994, 1998) to simulate the effects of different patch-removal strategies on owl occupancy rates under two different landscape models. The first model distinguished habitat as suitable versus unsuitable based on the presence of certain forest types, using the habitat map from Keitt and others (1995, 1997). The second model estimated habitat suitability in 9.7-mi² (25-km²) blocks, based on a combination of forest type and forest density. The authors found differences between landscape models in the effects of patch removal and differences between patch-removal strategies within landscape models. Similar to Keitt and others (1995, 1997), retention of certain spatially important patches that maintained connectivity buffered occupancy rates against habitat loss far more than retention of other patches. As long as connectivity among patches was maintained, simulated occupancy rates remained high even in the face of loss of significant amounts of habitat. But these conclusions rely largely on the assumption that maintaining a connected landscape will maintain dispersal processes regardless of population size. In reality, large losses in amount of habitat available to resident owls would result in fewer breeding owls and therefore fewer young to disperse. This ultimately could lead to the disconnection of subpopulations regardless of spatial aspects of connectivity.

Genetic Structure of Mexican Spotted Owl Populations

Knowledge of genetic structure of threatened populations also can aid in conserving and recovering those populations. Barrowclough and others (2006) investigated genetic structuring in Mexican spotted owl populations. Genetic diversity was high in most populations sampled, with approximately 17 and 7.5% of observed genetic variation distributed among populations and physiographic regions, respectively. Their data suggested substantial gene flow among populations sampled in the Mogollon Rim–Upper Gila Mountains region of central Arizona and New Mexico, with more restricted gene flow among other populations (Barrowclough and others 2006: Table 3, Figure 3). They recognized three major haplotypes within the range of the Mexican spotted owl. One haplotype was common in populations in the northwestern portion of the range and not found in the southeastern portion (black haplotype in fig. 30). A second haplotype (gray) was most common in the southeastern portion of the range, and not found in the northwestern portion. A third haplotype (white) was found in all populations studied, but was most common in the UGM RU and in southern Arizona. All three haplotypes occurred in populations within the UGM RU, suggesting that this area is important in facilitating

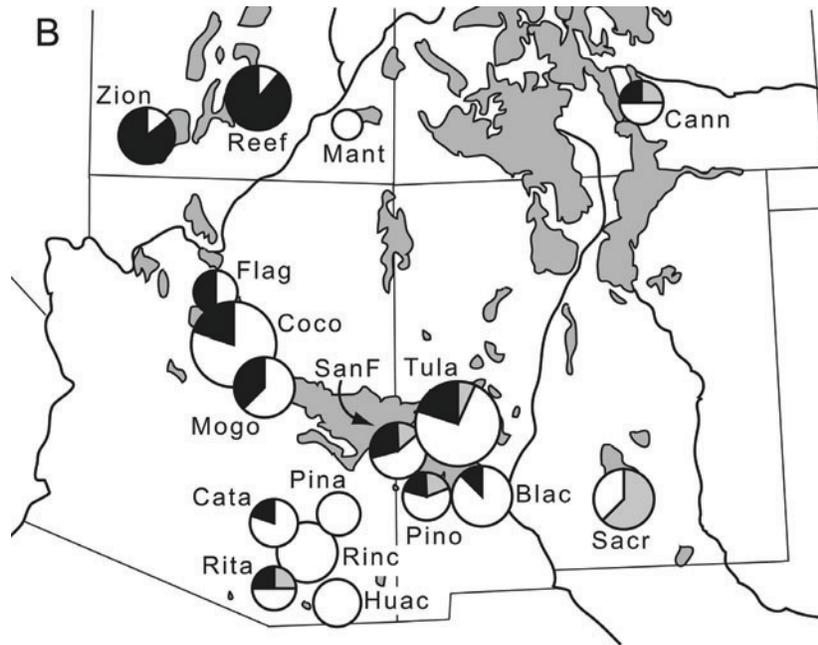


Figure 30. Genetic structure of the Mexican spotted owl population in the Southwestern United States. Proportions of three major haplotype clades (white, gray, and black) are indicated by pie-diagrams for 17 population samples. Area of pie is proportional to sample size. Shaded areas indicate approximate distribution of forested habitat, excluding pinyon-juniper. Reprinted from Barrowclough and others (2006: Figure 1). Used by permission from The American Ornithologists' Union.

gene flow across the range of the Mexican spotted owl. Barrowclough and others (2006) concluded that maintaining stepping stone habitat fragments between the large Upper Gila Mountains populations and other populations in the rest of the range would aid in maintaining viable populations of Mexican spotted owls. This strategy works only if the population in the UGM RU remains large enough to serve as a source population.

Summary—Metapopulation Ecology

The distribution of Mexican spotted owls throughout their range suggests a group of subpopulations that may function as a metapopulation. Landscape models evaluated by Keitt and others (1995, 1997) and Urban and Keitt (2001) all highlight the importance of landscape connectivity in maintaining stability within that metapopulation (see also Barrowclough and others 2006). Their findings highlight the importance of both large patches of habitat and of some small patches based on their location and consequent influence on landscape connectivity. The UGM RU is important in both contexts. This RU includes the largest contiguous area of habitat for Mexican spotted owls, and that is reflected in the large number of documented owls in that RU (Ganey and others 2004; see also fig. 7). This RU also is centrally located relative to other areas inhabited by Mexican spotted owls. The larger subpopulation in this RU likely serves as a core, source population for supplying new recruits to proximal outlying locations, and for facilitating gene flow throughout the range of the Mexican spotted owl.

Current Management Recommendations

Current recommendations for management of Mexican spotted owls and their habitat on National Forest System lands in Arizona and New Mexico were proposed in USDI FWS (1995) and formally adopted in all Southwestern National Forests through USDA FS (1996). This recovery plan is undergoing revision, and that revision likely will result in changes to management recommendations. But until a revised plan is completed and approved, recommendations in USDI FWS (1995) will continue to guide management. Briefly, these recommendations call for the following:

1. Designating Protected Activity Centers (PACs, minimum area = 600 ac [243 ha]) around occupied owl sites.
2. Managing a portion of the remaining landscape that supports mixed-conifer or pine-oak forest as replacement nest/roost habitat. USDI FWS (1995: Table II.B.1) called for managing 25 and 10% of the landscape in mixed-conifer and pine-oak forest, respectively, as replacement habitat in the UGM RU.
3. Managing areas around designated PACs so as to reduce the risk of stand-replacing fire on the landscape, thereby reducing the risk of such fire in adjacent protected habitats.
4. Retaining habitat elements within mixed-conifer and pine-oak forests important to the spotted owl and its prey.
5. Monitoring trends in the owl population and amounts of owl habitat.
6. Conducting research to understand how land-management activities affect Mexican spotted owls and their habitat.
7. Developing a long-term management plan.

USDI FWS (1995) explicitly recognized that designating and protecting PACs was a short-term (proposed as covering a 10 to 15-yr time period; USDI FWS 1995:80) strategy that did not address natural landscape dynamics. The Recovery Team concluded that available information about those landscape dynamics, and the effects of land-management activities on owls and their prey and habitat, was not sufficient to support a long-term management plan. The proposed strategy thus was intended to both protect occupied habitat and protect or enhance replacement roost/nest habitat while the knowledge necessary to support a more comprehensive long-term plan was gained.

Many of the recommendations in USDI FWS (1995) were never implemented. As a result, we still have no rigorous estimates of trends in owl populations or habitat, nor have we evaluated the effects of common land-management activities on owls or their prey and habitat. For the most part, land managers have chosen to manage around owl habitat (Beier and Maschinski 2003). This generally is consistent with the short-term protection of owl habitat called for in USDI FWS (1995) but has not advanced the goal of developing knowledge that

could be used to move beyond that short-term strategy. Thus, the uncertainties that limited our ability to devise a long-term, landscape-dynamics-based management strategy for Mexican spotted owls remain and will continue to remain until we proactively address some of the major information gaps identified.

Information Gaps

Although a number of studies have provided data on the status and ecology of Mexican spotted owls within the UGM RU, significant information gaps exist. Many aspects of basic ecology remain poorly known. For example, we still know little about the driving factors underlying population dynamics of spotted owls, and especially about how habitat composition and configuration influence population dynamics. In general, we have limited understanding of factors that limit Mexican spotted owl populations and/or how forest management may affect those factors.

The remaining information gaps are too numerous to treat comprehensively here. In the context of an effort such as 4FRI, there are two specific and related information gaps worthy of further discussion (see also Beier and Maschinski 2003). These are (1) lack of historical descriptions and reference conditions for spotted owl habitat, and (2) lack of information on effects of forest treatments on Mexican spotted owls and their habitat and important prey species.

As mentioned previously, historical information on Mexican spotted owls is anecdotal and sparse. Qualitative descriptions of areas occupied by owls suggest that they typically were observed in dense, shady stands of trees in mountains and canyons (for example, Ligon 1926). But structural conditions (for example, basal area, tree density, canopy cover) were never described for these areas, nor do historical accounts provide any information on spatial extent of the types of stands in which owls were observed. As a result, we have no quantitative information on stand structure and landscape composition in areas historically occupied by Mexican spotted owls. And, because we have no reference sites currently occupied by Mexican spotted owls where the natural fire cycle has been maintained, all available quantitative information on stand structure and landscape pattern in owl habitat derives from forests subject to some level of fire suppression. We know that structure and composition of forests within the range of the owl, especially ponderosa pine and drier mixed-conifer forests, has changed markedly since the advent of effective fire suppression (Cooper 1960, Dieterich 1983, Covington and Moore 1994, Fulé and others 1997, 2002, 2003, 2004, 2009, Cocks and others 2005). Logically, this should include stands occupied by spotted owls.

Current data indicate that owls within the UGM RU are most common in mixed-conifer and ponderosa pine–Gambel oak stands with high basal area and canopy cover. These stands frequently have a prominent hardwood component and numerous large trees and snags. Most are uneven-aged, with variable age- and size-classes of trees and snags and considerable volumes of down logs. These are not the kinds of

stand structures that forest managers typically try to create in restoration activities in ponderosa pine and mixed-conifer forests that evolved with relatively frequent fire (for example, Cooper 1960, Dieterich 1983, Covington and Moore 1994, Fulé and others 1997, 2002, 2003, 2004, 2009, Cocke and others 2005, Kaufmann and others 2007; see also Beier and Maschinski 2003). The conditions typical of owl nesting and roosting habitat therefore are frequently viewed as “unsustainable” and unnatural in these systems (Johnson 1994). How then did Mexican spotted owls, which apparently occurred historically in these forest types (for example, Ligon 1926, Steele 1927, Bailey 1928, Huey 1930), come to specialize on these types of forest stands (for example, Hutto and others 2008)? Were such stands (or perhaps patches smaller than stands) present historically in these landscapes, for example in fire refugia (Camp and others 1997) such as north-facing slopes or rocky canyon slopes? If so, is there a minimum size to suitable patches for nesting and/or roosting owls? Or were spotted owls able to exist and persist in stands with lower basal area, canopy cover, and fuel loads?

These are important (and not mutually exclusive) questions. If such stands, or smaller patches with similar features, occurred naturally in historical landscapes under natural fire regimes, then maintaining similar patches for spotted owls should be an objective in forest restoration projects. The management issue then becomes how much of such habitat is enough to support owls, how large should patches of such habitat be, how should those patches be arranged on the landscape to support owls, and how can those considerations best be balanced with managing fuels and risk of large wildfires on the landscape? The fuels aspect of this suite of questions can be answered through simulation modeling, whereas the questions relating to sufficient amounts and arrangement of owl habitat are more intractable. Although simulation modeling also could provide some insights here, those questions ultimately can be answered only by monitoring owl populations over time in landscapes with different amounts and arrangement of habitat.

If, however, spotted owls historically occupied stands with lower basal area, canopy cover, and fuel loads, it suggests that management for reduced levels of stand variables typically associated with Mexican spotted owl habitat may be compatible with maintaining habitat for spotted owls. That is, it may be possible to manage for lower basal area, canopy cover, and fuel loads yet still provide habitat for spotted owls, especially in stands featuring large trees. The problem is that we do not know where potential thresholds may lie, or how far we can reduce stand conditions before those stands no longer provide habitat for spotted owls. This question can best be answered in an experimental framework, by implementing treatments to reduce these stand conditions and monitoring owl response over time.

The 4FRI effort could provide a valuable opportunity to begin answering these questions. The large-scale nature of this project provides unique opportunities to apply different landscape-design strategies and within-stand treatment levels, and to incorporate sufficient numbers of owl territories to evaluate owl response variables effectively. Given the threatened status of the Mexican spotted owl, and the importance of the owl population within the UGM RU

to landscape connectivity (Keitt and others 1997, Urban and Keitt 2001) and gene flow (Barrowclough and others 2006) within the larger range of the owl, managers should proceed cautiously and ensure that rigorous monitoring and appropriate feedback loops are implemented as part of the treatment design.

Currently available data can be used in this process, especially to define initial thresholds for owl habitat. In fact, we provide some preliminary suggestions in this report. Another potential source of valuable information may exist where owls occur in large roadless areas within the Gila National Forest. Although these areas do not have a completely intact fire regime, there are areas that have burned multiple times. Evaluating structural conditions in patches used by owls for roosting and especially nesting in such areas also may provide insights into potential thresholds (Ganey and others 2008). Similarly, evaluating landscape composition in those areas may provide information on appropriate patch sizes and spatial arrangement of patches, two important parameters for landscape design strategies. In theory, such an analysis could be conducted without extensive field work, provided that rigorous information on owl locations is available as well as satellite imagery from the appropriate years.

Conclusions

The UGM RU appears to harbor a key population of Mexican spotted owls. More than half of the known population resides within this RU, and the widely distributed forests within this RU appear to foster high internal landscape connectivity. In addition, because of its central location and large size, this population appears to be important in terms of owl movements and gene flow across the larger range. No current data is available on owl population trends, but all populations studied within the UGM RU were declining during the 1990s.

Owls in this RU reside primarily in mixed-conifer and ponderosa pine–Gambel oak forests in mountain and canyon systems. Forests occupied typically feature high basal area and canopy cover and large trees. Maintaining these stand characteristics in conjunction with reducing fuel loads and restoring southwestern forests presents special challenges for land managers. Landscape-scale simulations suggest that, at least in some landscapes, fire risk can be managed effectively without extensive management within owl habitat (Prather and others 2008). This type of strategy may not be optimal in the long term, as it leaves owl habitat in a fire-prone condition. Available data on owl space and habitat use, as well as on habitat relationships of key prey species, can aid managers faced with maintaining or enhancing spotted owl habitat. Considerable uncertainty remains over exactly what constitutes owl habitat, how much habitat is required to sustain a viable population, and how that habitat should be arranged on the landscape. Reducing that uncertainty will require learning by doing. Because of its large spatial scale, the 4FRI project provides a unique opportunity to incorporate spotted owls and their habitat in landscape-scale planning and to answer questions about habitat thresholds and the effects of forest management on Mexican spotted owls and their habitat.

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Appendix 1. Common and scientific names of species mentioned in the text.

Common name	Scientific name
Birds	
Barred owl	<i>Strix varia</i>
California spotted owl	<i>Strix occidentalis occidentalis</i>
Great horned owl	<i>Bubo virginianus</i>
Mexican spotted owl	<i>Strix occidentalis lucida</i>
Northern goshawk	<i>Accipiter gentilis</i>
Northern spotted owl	<i>Strix occidentalis caurina</i>
Swainson's warbler	<i>Limnothlypis swainsonii</i>
Mammals	
Brush mouse	<i>Peromyscus boylii</i>
Botta's pocket gopher	<i>Thomomys bottae</i>
Deer mouse	<i>Peromyscus maniculatis</i>
Elk	<i>Cervus elaphus</i>
Golden-mantled ground squirrel	<i>Spermophilus lateralis</i>
Gray-collared chipmunk	<i>Tamias cinereicollis</i>
Long-tailed vole	<i>Microtus longicaudus</i>
Mexican woodrat	<i>Neotoma mexicana</i>
Mogollon vole (formerly Mexican vole)	<i>Microtus mogollonensis</i> <i>Microtus mexicanus</i>
Rock squirrel	<i>Spermophilus variegatus</i>
Rabbits	<i>Sylvilagus</i> spp.
White-footed mouse	<i>Peromyscus</i> spp.
Woodrats	<i>Neotoma</i> spp.
Plants	
Arizona cypress	<i>Cupressus arizonica</i>
Blue spruce	<i>Picea pungens</i>
Box elder	<i>Acer negundo</i>
Douglas-fir	<i>Pseudotsuga menziesii</i>
Dwarf mistletoe	<i>Arceuthobium</i> spp.
Engelmann spruce	<i>Picea engelmannii</i>
Gambel oak	<i>Quercus gambelii</i>
Junipers	<i>Juniperus</i> spp.
Limber pine	<i>Pinus flexilis</i>
Narrowleaf cottonwood	<i>Populus angustifolia</i>
New Mexico locust	<i>Robinia neomexicana</i>
Pinyon pine	<i>Pinus edulis</i>
Ponderosa pine	<i>Pinus ponderosa</i>
Quaking aspen	<i>Populus tremuloides</i>
Southwestern white pine	<i>Pinus strobiformis</i>
White fir	<i>Abies concolor</i>
Willows	<i>Salix</i> spp.

Appendix 2. Study areas and associated studies in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico.

Study area	Location	Methodology ¹	Objectives ²	Cover types ³	Products ⁴
CNF	Coconino Natl. For., AZ	MR, RT	D, PT, HS, JD	PO, PP, MC, PJ,	1
GNF	Tularosa Mtns., NM	MR	D, PT, HS	MC, PP, PJ	2
BR	Black Range, NM	MR	D, PT	U	3
MM	Magdalena Mtns., NM	MR	D, PT	U	3
SMM	San Mateo Mtns., NM	MR, RT	D, PT, JD, HS	PP, PJ, MC, R	3, 4
UGM	Upper Gila Mountains RU	MR	A	Highly variable	5
SFP	San Francisco Peaks, AZ	RT	HR, HS	MC, PP, PP/Oak/J	6
WC	Walnut Canyon, AZ	RT	HR, HS	MC, PP, PP/Oak/J	6
WM	White Mtns., AZ	RT	HR, HS	MC, PP	6
BMC	Bar-M Canyon, AZ	RT	HR, HS, IC, PA	PO, PP, Meadow	7

¹ Methodology: MR = mark-recapture; RT = radio-telemetry.

² Primary study objectives: A = estimate abundance of spotted owls; D = demography (estimate survival and reproductive rates); IC = study competitive interactions with great horned owls; JD = study natal dispersal of juvenile owls; PA = estimate prey abundance; PT = estimate population trend; HR = estimate home-range size; HS = study habitat selection.

³ Dominant cover types within study area: MC = mixed-conifer forest; PJ = pinyon-juniper woodland; PO = pine-oak forest; PP = ponderosa pine forest; PP/Oak/J = ponderosa pine-oak-juniper on rocky canyon slopes. The UGM study included 25 separate study areas across the UGM RU, with dominant cover types varying greatly among study areas. Cover types are described in Appendix 3.

⁴ Products: Published papers resulting directly from or contributed to by data from this study area: 1 = Hunter and others 1994, Grubb and others 1997, Ganey and others 1998, Seamans and Gutiérrez 1999, Seamans and others 1999, 2002, May and Gutiérrez 2002, Hampton and others 2003, Ganey 2004, May and others 2004, Sisk and others 2006, Prather and others 2008; 2 = Hunter and others 1994, Seamans and Gutiérrez 1995, 1999, Gutiérrez and others 1996, Peery and others 1999, Seamans and others 1999, 2002; 3 = Stacey and Peery 2002, Stacey 2010; 4 = Arsenault and others 1997, Stacey and Hodgson 1999; 5 = Ganey and Benoit 2002, Hampton and others 2003, Ganey and others 2004, 2008, Sisk and others 2006, Prather and others 2008; 6 = Ganey 1990, 1992, Ganey and Balda 1989b, 1994, Ganey and Benoit 2002, Hampton and others 2003, Ganey and Block 2005a, Sisk and others 2006, Prather and others 2008; 7 = Ganey and others 1997, 1999, 2000, 2003, Ganey and Benoit 2002, Hampton and others 2003, Block and others 2005, Ganey and Block 2005a, b, Sisk and others 2006, Prather and others 2008.

**Appendix 3. Species composition of major cover types
as used in this report. Scientific names for species
are provided in Appendix 1.**

Cover type	Dominant species	Associated species
Meadow	Grasses, forbs	Occasional ponderosa pine or Gambel oak tree
Mixed-conifer forest	Douglas-fir, white fir, ponderosa pine	Southwestern white pine, limber pine, quaking aspen, Gambel oak, Engelmann spruce, blue spruce
Montane meadow	Grasses, forbs	
Pinyon-juniper woodland	Pinyon pine, various junipers	Ponderosa pine, Gambel oak
Ponderosa pine–Gambel oak	Ponderosa pine, Gambel oak	Pinyon pine, various junipers ¹ oak forest
Ponderosa pine forest	Ponderosa pine	Gambel oak, pinyon pine, various junipers
Ponderosa pine-oak-juniper	Ponderosa pine, Gambel oak,	Various junipers, pinyon pine, Douglas-fir
Riparian forest	Box elder, narrowleaf cottonwood	Species associated with surrounding upland types
Xeric forest	Ponderosa pine, pinyon pine, various junipers and oaks	Occasional Douglas-fir or white fir

¹These species generally are rare in this cover type, compared to the ponderosa pine-oak-juniper cover type. Ponderosa pine–Gambel oak forest also has a stronger component of tree-form Gambel oak than ponderosa pine forest.



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