APPENDIX B - ECOLOGY OF THE MEXICAN SPOTTED OWL

This Appendix provides details on the biology and ecological relationships of the Mexican spotted owl (*Strix occidentalis lucida*). These details provided the background for recovery planning, but a lengthy discussion of ecology in the body of this Recovery Plan was considered too distracting. Thus, we provide the information here for the interested reader.

This Appendix is intended to be an overview of this subspecies’ biological characteristics and ecological relationships germane to recovering its populations. Emphasis is placed on information developed since the original Recovery Plan was published (USDI FWS 1995). Although major information gaps still exist, our understanding of the Mexican spotted owl’s natural history has increased since 1995. In particular, the number of sites known to be occupied by Mexican spotted owls in canyon environments has greatly increased since that time. Thus, we also provide additional detail about the ecology of canyon-dwelling individuals, particularly when different from other Mexican spotted owls.

We have included results from both published and unpublished references, based on a search of the literature through 15 Dec 2011. Although we prefer to rely on published information, considerable information regarding the Mexican spotted owl resides in unpublished reports. This summary is not exhaustive, because it is impossible to include or even locate every unpublished report. We have attempted to make it reasonably comprehensive, however, realizing that most biologists, resource managers, or other interested parties may not have time to locate and read the numerous references summarized here. In addition, a wealth of information exists for two other subspecies of spotted owls. Although different in some respects, many aspects of the owl’s biology and ecology are similar among subspecies. Where appropriate, information from other subspecies was included for comparison or where data were limited regarding the Mexican subspecies.

1. **Taxonomy and Genetics**

   **A. Systematics**

   Knowledge of taxonomic relationships of threatened species is critical to their protection and recovery, particularly where protection is based on subspecific status, as is the case with the Mexican spotted owl. This owl is one of three subspecies of spotted owl recognized by the American Ornithologists’ Union (AOU) in its last checklist that included subspecies (AOU 1957:285). The other two subspecies are the northern (*S. o. caurina*) and the California (*S. o. occidentalis*) spotted owls.

   Taxonomists have debated the systematics of the Mexican spotted owl for decades. The Mexican subspecies was first described from a specimen collected at Mount Tancitaro, Michoacán, Mexico and named *Syrnium occidentale lucidum* (Nelson 1903). All subspecies of spotted owl were later assigned to the genus *Strix* (Ridgway 1914) and the subspecific name for the Mexican spotted owl was changed to *lucida* to conform to taxonomic standards. Swarth (1910, 1914) split the Arizona population of spotted owls out as *S. o. huachucae*, noting that they were paler than *S. o. lucida*. Ridgway (1914) applied the name *huachucae* to owls from Arizona east to the Guadalupe Mountains in Texas. In contrast, Oberholser (1915) concluded
that *huachucae* was a synonym of *lucida*, and this taxonomic designation was followed by the AOU (1957). Monson and Phillips (1981) continued to recognize *huachucae* for Arizona owls, however, and Dickerman (1997) split the Mexican spotted owl into three subspecies, based on plumage differences noted in an examination of museum specimens. He proposed recognizing owls from the southwestern U.S. and northern Mexico (Sonora and Chihuahua) as *huachucae*, with a new subspecies, designated as the volcano owl (*S. o. juanaphillipsae*), recognized in the state of Mexico, and *lucida* occurring between the ranges of *huachucae* and *juanaphillipsae*. This debate over the subspecific status of the Mexican spotted owl continues today (Haig et al. 2004a, Funk et al. 2008).

The Mexican subspecies is geographically isolated from both the California and northern subspecies (Fig. B.1), with only a trace of historical genetic contribution within the range of the northern spotted owl (Funk et al. 2008). Using electrophoresis to examine allozyme variation, Barrowclough and Gutiérrez (1990) found a major allelic difference between the Mexican spotted owl and the two coastal subspecies. They concluded from this difference that the Mexican spotted owl was isolated genetically from the other subspecies for considerable time, has followed a separate evolutionary history, and therefore could be considered a separate species (Barrowclough and Gutiérrez 1990:742). Most other recent studies (Barrowclough et al. 1999, Haig et al. 2001, Funk et al. 2008), as well as a recent review of all published and unpublished genetic data (Fleischer et al. 2004) also supported designation of the Mexican spotted owl as an Evolutionarily Significant Unit. In a somewhat divergent view, Haig et al. (2004a) found little evidence to support subspecific differences between the California and Mexican subspecies on the basis of molecular genetics. Nevertheless, they suggested that these populations should be managed separately because of their current geographic separation (Haig et al. 2004a). Most recently, Funk et al. (2008) reported evidence of introgression of Mexican spotted owls into the northern portion of the range of the northern spotted owl, and suggested that this resulted from long-distance dispersal of Mexican spotted owls. We are unsure how to interpret these results, as this would require dispersal over distances that greatly exceed any documented movements of spotted owls, and no other studies have reported similar findings. Funk et al. (2008) supported recognition of three subspecies of spotted owls despite this introgression, however.

Two other species within the genus *Strix* occur north of Mexico: barred (*S. varia*), and great gray (*S. nebulosa*) owls. The great gray owl is a northern species that does not occur within the range of the Mexican spotted owl. Historically, barred owls also did not occur in sympathy with Mexican spotted owls within the U.S. However, unconfirmed sightings of both species have been reported from the vicinity of Big Bend National Park in southern Texas in recent times (Wauer 1996), and there are recent confirmed records of barred owls in northern and eastern New Mexico (Williams 2005, cited in Cartron 2010; H. Walker, NMGFD, pers. comm.). Whether these confirmed records indicate a range expansion by barred owls or simply vagrant individuals is unknown at this time.
Figure B.1. Range map of three subspecies of spotted owls.
Mexican spotted, barred, and fulvous (*S. fulvescens*) owls all occur in Mexico, and they are sometimes considered as a “superspecies” (Holt et al. 1999:199-200). The ranges of the Mexican spotted and barred owl may or may not overlap in Mexico (Williams and Skaggs 1993, Howell and Webb 1995); little is known about local distributional patterns and habitats occupied in this zone of apparent overlap (Enriquez-Rocha et al. 1993). The fulvous owl does not appear to be sympatric with Mexican spotted owls in Mexico (but it may overlap the distribution of the barred owl slightly, Holt et al. 1999:198-200).

Patterns of range overlap may have significant implications for Mexican spotted owls. Barred owls are known to hybridize with northern spotted owls in the Pacific Northwest (Hamer et al. 1994; Dark et al. 1998; Haig et al. 2004b; Kelly and Forsman 2004; Funk et al. 2007; also see Gutiérrez et al. 2004, 2007). This hybridization is occurring in a relatively recent zone of contact caused by a rapid range expansion by barred owls into the range of the northern spotted owl in the Pacific Northwest (Taylor and Forsman 1976; Dark et al. 1998; Kelly 2001; Gutiérrez et al. 2004, 2007). Both hybrids between spotted and barred owls and backcrosses between these hybrids and the parental types have been found throughout much of the range of the northern spotted owl.

The implications of this hybridization for populations of northern spotted owls are currently unknown. Genetic analyses clearly indicate that spotted and barred owls are distinct species with no indication of previous gene flow across species boundaries (Haig et al. 2004b, Funk et al. 2007). Closely related species occasionally hybridize naturally, especially where habitat disruption has led to contact between previously geographically isolated species (Short 1965, 1972). Kelly and Forsman (2004) noted that relatively few hybrids of spotted and barred owls have been identified to date, and they suggested that other isolating mechanisms (e.g., behavior or habitat selection) may be working effectively to maintain hybridization at low levels.

Holt et al. (1999:198) reported occasional hybridization between spotted and barred owls in Mexico but did not elaborate on sources for this information. Given the situation in the recent zone of contact discussed above for the Pacific Northwest, it seems likely that hybridization between Mexican spotted and barred owls could increase if barred owls expand their range further into the range of the Mexican spotted owl. For discussion of other potential interactions between spotted and barred owls, see *Interspecific Competition*.

**B. Genetic Structure of Mexican Spotted Owl Populations**

Knowledge of genetic structure of threatened populations can aid in conserving and recovering those populations. Barrowclough et al. (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 (UGM) region of central Arizona and New Mexico, with more restricted gene flow among other populations. The relatively dense population in the Sacramento Mountains showed evidence of isolation from other populations. Barrowclough et al. (2006) concluded that viability of the Sacramento Mountains population depends largely on internal population dynamics, suggesting that
managers should maintain sufficient habitat to support a viable population in this range. Some smaller populations appeared to depend on immigration from larger concentrations of owls in the UGM region. Barrowclough et al. (2006) concluded that maintaining stepping stone habitat fragments between the large UGM populations and other populations in the rest of the range would aid in maintaining viable populations of Mexican spotted owls (see additional discussion in sections on Landscape Connectivity and Metapopulation Ecology).

2. Description

A. Appearance

All three subspecies of the spotted owl are mottled in appearance with irregular white and brown spots on its otherwise brown abdomen, back, and head (Gutiérrez et al. 1995). White spotting on brown breast feathers is one characteristic that distinguishes the spotted owl from the barred owl, which has brown and white vertical streaks on its breast (Fig. B.2). Both spotted and barred owls have dark eyes in contrast to other medium to large North American owls that have lighter colored irises (the small flammulated owl [Otus flammeolus] also has dark irises). Both spotted and barred owls lack external ear tufts, and the head has a rounded appearance. The large round facial disk has indistinct concentric circles around both eyes.

The three subspecies of spotted owls exhibit color variation in their body plumage. White spots of the Mexican spotted owl are generally larger and more numerous than in the other two subspecies, giving it a lighter appearance (Strix occidentalis translates as “owl of the west” and lucida means “light” or “bright”; Ganey 1998). Both remiges (wing feathers) and retrices (tail feathers) are dark brown barred with lighter brown and white.

Adult male and female spotted owls are mostly monochromatic in plumage, but several age classes can be distinguished by plumage (Forsman 1981, Moen et al. 1991). Juvenile spotted owls (hatching to approximately five months) have a downy appearance (Fig. B.2), which persists around the head even after the flight feathers grow in (i.e., until late August or September of their hatch year). Subadults (5 to 26 months) closely resemble adults but have pointed retrices with a pure white terminal band (Forsman 1981, Moen et al. 1991). Two age classes of subadults (first- and second-year, respectively; Fig. B.3) generally can be recognized, based on the amount of wear to the tips of the retrices and the date of observation (Moen et al. 1991). The retrices of adults (>27 months) have rounded tips, and the terminal band is mottled brown and white (Fig. B.3).

The spotted owl is a medium-sized owl and ranks fifth largest among the 19 North American owl species (Johnsgard 1988). Like many other raptors, spotted owls exhibit reversed sexual dimorphism where females are larger than males. Adult male Mexican spotted owls (n = 68) average 509 ± 33 (SD) g, and adult females (n = 68) average 569 ± 44 g (Gutiérrez et al. 1995). There appears to be clinal variation among the three subspecies in a number of morphological characteristics, with size (or mass) generally largest in the northern subspecies, intermediate in the California subspecies, and smallest in the Mexican subspecies (Gutiérrez et al. 1995).
Figure B.2. Appearance of adult Mexican spotted (top left) and barred (top right) owls. Note spotting on the breast of the Mexican spotted owl versus vertical barring on the breast of the barred owl. Lower photo shows a juvenile (young of the year) with downy body plumage. Compare downy head of juvenile to head of female adult visible behind the juvenile. Photos: Top left: J. L. Ganey, Bottom: J. P. Ward, Jr. Barred owl photo downloaded from: http://www.fws.gov/southeastlouisiana/images/habitat_mgt_images/barred_owl.jpg.
Figure B.3. Photos showing tips of tail feathers of three age classes of spotted owls with non-downy body or head plumage (photos from Moen et al. 1991). From left to right are: first-year subadult (note tips are pointed and tufted, and terminal band is pure white); second-year subadult (note tips are pointed and retain the pure white terminal band, but tufts have worn away); and, adult (note rounded tip, and mottled brown spots in white terminal band). Young of the year also have pointed and tufted tips but also have downy body or head plumage.

B. Vocalizations

The spotted owl, being territorial and primarily nocturnal, is heard more often than seen. It has a wide repertoire of calls (Forsman et al. 1984, Ganey 1990), most of which are relatively low in pitch and composed of pure tones (Fitton 1991). The low frequencies and pure tones characteristic of these calls suggest that they are well-suited for accurate long-distance communication through areas of relatively dense vegetation (Fitton 1991, see also Morton 1975, Forsman et al. 1984). This likely is important in a nocturnally active animal that ranges over large areas and that needs to communicate effectively with both its mate and neighboring owls across large distances (Ganey 1990).

Male and female spotted owls can be distinguished by their calls. Males have a deeper voice than females (Forsman et al. 1984) and generally call more often than females (Ganey 1990). There also appears to be intrasexual variation in calling rates (Laymon 1988, Ganey 1990).

Forsman et al. (1984) described 14 calls for the northern spotted owl, at least 10 of which also are used by Mexican spotted owls in Arizona (Ganey 1990). Both sexes use most calls, but the frequency with which call types are used varies among sexes (Forsman et al. 1984). The most common vocalization, used more often by males (Ganey 1990, Kuntz and Stacey 1997), is a series of four unevenly spaced hoots (four-note location call; Forsman et al. 1984, see also Fitton 1991). Females frequently use a clear whistle ending with an upward inflection (contact call; Forsman et al. 1984) as well as a series of sharp barks (bark series; Forsman et al. 1984, Ganey 1990).

Mexican spotted owls call mainly from March to November and are relatively silent from December to February (Ganey 1990). Calling activity increases from March through May (although nesting females are largely silent during April and early May) and then declines from June through November (Ganey 1990). Ganey (1990) reported that calling activity was greatest
during the 2-hour period following sunset, with smaller peaks 4 to 8 hrs after sunset and just before sunrise.

Mexican spotted owls studied by Ganey (1990) called more than expected during the last quarter and new moon phases of the lunar cycle, and they called most frequently on calm, clear nights when no precipitation was falling. Forsman (1983) reported that northern spotted owls also called most frequently on calm, clear nights, whereas the generality of the relationship between moon phase and calling rates is unknown. Calling bouts of Mexican spotted owls lasted approximately twice as long when the focal owls’ mate also was calling and over three times as long when “other” owls were calling (Ganey 1990). In most cases, the other owls calling were neighboring Mexican spotted owls or great horned owls (*Bubo virginianus*).

Fitton (1991) and Kuntz (1998) studied variability among calls of spotted owls in northwestern California and New Mexico, respectively. Fitton (1991) found significant differences between call structure of neighboring and non-neighboring owls, with variance in call structure lower among neighboring owls than among non-neighbors. Similarly, Kuntz (1998) identified population-level differences among calls of populations of Mexican spotted owls in different mountain ranges. These findings suggest that spotted owls are able to use vocal learning to make fine adjustments to call structure (Fitton 1991). This development of a local dialect could allow owls to identify their neighbors without needing to be able to identify specific individuals. The ability to distinguish neighbors from non-neighbors by calls could provide a means to identify intruders, and thus trigger territorial defense when it is most needed. The ability to distinguish between neighboring and non-neighboring owls could be particularly important if owls are not able to identify individuals by their calls. Whether or not these owls can identify individuals by their calls is unknown at this time. However, researchers can recognize individual male Mexican spotted owls using multivariate analysis of call structure (Kuntz 1998). Given the frequent vocal communication that occurs between mated owls during the nesting season, and the overall importance of vocal communication to a nocturnal, territorial animal, we would be surprised if spotted owls could not identify individuals by their vocalizations.

The fact that spotted owls are territorial and respond to calls is important in the context of research and management. Acoustic lure surveys (Reid et al. 1999) are used to locate owls for both research and management activities (see Appendix D: Survey Protocol). These surveys are proven to be effective at locating spotted owls (Reid et al. 1999), but the influences of factors such as topography, vegetation, and distance on survey effectiveness are poorly understood. In a preliminary analysis, Bowles et al. (2002) demonstrated that Mexican spotted owls could be detected at distances up to 2 km (1.2 mi) under ideal conditions but that topography and ambient noise greatly affected detection distance (see also Denes et al. 2006). They suggested that incorporating the effects of such factors could improve estimates of effective area surveyed and inform survey protocols.

### 3. Distribution

The Mexican spotted owl occurs in forested mountains and rocky canyonlands throughout the southwestern U.S. and Mexico (Ligon 1926, Gutiérrez et al. 1995, Ward et al. 1995). It ranges from Utah, Colorado, Arizona, New Mexico, and the western portions of Texas south into
several States of Mexico (Fig. B.1). While this owl occupies a broad geographic area, it does not occur uniformly throughout its range (Ward et al. 1995). Instead, the owl occurs in disjunct areas that correspond with isolated mountain ranges and canyon systems (Fig. B.4).

The current distribution of Mexican spotted owls generally mimics its poorly known historical extent, with some exceptions (Ward et al. 1995). For example, the owl has not been reported recently as a breeding species from riparian corridors along most low- or mid-elevation rivers and creeks in Arizona and New Mexico (although it does use these areas during winter; see Movements and Migration, below). Nor has it been reported in recent times from historically occupied areas of southern Mexico (Williams and Skaggs 1993, Ward et al. 1995) or from some areas where recent habitat models suggest these owls should occur in canyons (see Habitat Models, below). Riparian communities and many previously occupied localities in the southwestern U.S. and southern Mexico have undergone significant habitat alteration since the historical sightings (USDI FWS 1993). These areas, when occupied, likely aided in maintaining connectivity among populations throughout the southwest.

In the United States, the majority of owls are found on U.S. Forest Service (FS)-administered lands (Table B.1). Exceptions to this general pattern occur in parts of the Colorado Plateau (CP) and Basin and Range-East (BRE) Ecological Management Units (EMUs), where owls are found primarily in rocky canyons on lands administered by the National Park Service (NPS) and Bureau of Land Management (BLM).

Surveys conducted since the 1995 Recovery Plan continue to locate new owl sites and increase our knowledge of owl distribution, but not necessarily of owl abundance. For example, 758 owl sites were recorded for the period 1990–1993 (Ward et al. 1995). During a recent review for establishing Critical Habitat, 1,222 owl sites were recorded for the period 1990–2004 (USDI FWS 2004). A more recent tally through 2008 indicated 1,301 cumulative sites occupied by one or more Mexican spotted owls (Table B.1). This increase is mainly a product of new surveys being completed within previously unsurveyed areas, however. This tally represents a cumulative tally of all sites where Mexican spotted owls have been located over time, does not provide any information on how many of those sites are occupied at any particular time, and does not account for any known sites lost due to high-severity wildland fire or natural site-extirpation processes. Thus, an increase in abundance cannot be inferred from these data. Likewise, the distribution of owl sites alone cannot indicate population density in various areas and may be more indicative of differences in survey effort than in owl density.

Information on the current status of Mexican spotted owls in Mexico is limited. This subspecies has been reported to occur within the mountain ranges of five general regions distributed through the Mexican states of Chihuahua, Sonora, Durango, Jalisco, Michoacán, Guanajuato, Sinaloa, San Luis Potosi, Nuevo Leon, Coahuila, Colima, and Aguascalientes (Williams and Skaggs 1993, Ward et al. 1995, Tarango et al. 2001). The majority of owls have been located in the Sierra Madre Occidental range, including in Sonora, Chihuahua, Sinaloa, Durango, Aguascalientes, and Zacatecas, and in the Sierra Madre Oriental range, including in Coahuila, Nuevo Leon, and San Luis Potosi; fewer have been found in the Transverse Volcanic Range in
Figure B.4. General areas occupied by Mexican spotted owls within five EMUs within their range in the United States.
Table B.1. Number of Mexican spotted owl site records summarized by U.S. EMU and land ownership. Numbers are cumulative since 1989. A site could include a single owl or a pair of owls. These numbers are best interpreted as minimum cumulative numbers of locations where at least one owl was recorded during at least one breeding season since 1989. We do not know how many of these sites are currently occupied. Data are from USDA FS-PAC centers, Ward et al. (1995), Mullet (2008), and site locations provided by several people to the authors of this Recovery Plan.

<table>
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<th>Site records¹</th>
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<th>% of total</th>
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¹ Site as defined in Box 1 of the Recovery Plan.
² Colorado portion = 21 sites; New Mexico portion = 53 sites.

Jalisco, Michoacán, Guanajuato, and the state of Mexico (Williams and Skaggs 1993, USDI FWS 1995). Parts of the northern Sierra Madre area are similar ecologically to the Sky Island Mountains of southeastern Arizona (Marshall 1957, Cirett-Galan and Diaz 1993). It is not known if the distribution of Mexican spotted owls in Mexico has changed or how many additional sites have been recorded since 1994.
4. Habitat Use

The term habitat can convey many meanings (for a comprehensive discussion of the habitat concept as it applies to birds, see Block and Brennan 1993). Here, we follow the terminology summarized by Hall et al. (1997) and use the term habitat to mean the physical elements and biological resources required by the Mexican spotted owl to persist. This generalized definition includes climatic ranges, types of vegetation, food items, and non-biotic or physical features like topography or geologic structures. Habitat for a given organism is often explicitly defined by vegetative categories like cover-types with the implicit understanding that these categories are comprised of multiple resources that vary among categories. As organisms use habitats to meet multiple life history requirements, 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. In the following sections, we describe Mexican spotted owl habitat according to scale and activity.

A. Landscape Scale

This owl’s habitat occurs as patches within uninhabitable portions of a larger land base. The term landscape refers to the combined space of habitat patches and a matrix of unusable areas. For Mexican spotted owls to persist through time, there must be adequate dispersion of individuals throughout the landscape and a means for population connectivity. In addition, dispersing owls must be able to locate usable habitat if they are to survive and reproduce. Use of habitat at the landscape scale, then, includes use of patches and corridors for assuring connectivity among subpopulations as well as patch use by resident birds that form local populations. Here, we first discuss studies of landscape connectivity, then focus on studies of landscape composition around owl use areas (see also Home Range Features and Microhabitat Features).

a. Landscape Connectivity.—Keitt et al. (1995, 1997) attempted to identify those 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, and second, they modified this approach to emphasize positional effects (i.e., small clusters that are important because they act as “stepping stones” or bridges between larger habitat clusters).

In the first analysis, the largely contiguous forest habitat of the Mogollon Rim (UGM EMU) emerged as most important overall, because of its large area. In the analysis emphasizing cluster position, the UGM EMU again emerged as important, due to its central location. But a few small habitat clusters also emerged as particularly important. These included several fragments of the Cibola National Forest (Mount Taylor and Zuni Mountains, CP EMU) that may serve as stepping stones between other, larger clusters. These small patches may warrant particular management attention; they may be important to overall landscape connectivity despite supporting relatively few resident owls. However, conclusions about the importance of specific habitat clusters depend heavily on the underlying map of habitat clusters, and the true distribution of these clusters remains unknown.
In a separate analysis, 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 (see Metapopulation Ecology, below) and used Hanski’s incidence function (Hanski 1994, 1998) to simulate the effects of different patch-removal strategies on owl occupancy rates according to 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 et al. (1995, 1997). The second landscape model estimated habitat suitability in 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 landscapes. Similar to their earlier analysis (Keitt et al. 1995, 1997), retention of certain patches that maintained connectivity buffered occupancy rates against habitat loss far more than removal of other, less spatially important patches. As long as connectivity among patches was maintained, occupancy rates remained high even in the face of loss of significant amounts of habitat. However, 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 owls that could reproduce and fewer young to disperse. This ultimately could lead to the disconnection of subpopulations regardless of spatial aspects of connectivity.

In summary, Keitt et al. (1995, 1997) and Urban and Keitt (2001) evaluated landscape models that all highlight the importance of landscape connectivity (see also Barrowclough et al. 2006). Their findings further highlight the importance of both large patches of habitat, and of some small patches based on their location and consequent influence on landscape connectivity. Their results suggest that management plans should be concerned with those stepping-stone areas, and that conservation efforts focused in those areas may pay large dividends relative to land area involved in conservation measures. We view this general conclusion as robust to violations of model assumptions, although the specific patches involved obviously depend on those assumptions.

b. Landscape Composition.—Understanding landscape composition of sites occupied by Mexican spotted owls clearly would aid in developing conservation strategies for this species. To date, three studies have examined landscape composition around sites occupied by Mexican spotted owls at various spatial scales. These studies are discussed below.

Grubb et al. (1997) used air-photo interpretation to compare relative area of four canopy-cover classes between 47 owl nest and randomly located sites on the Coconino National Forest, north-central Arizona, at five different spatial scales. They analyzed landscape composition in both circles (radii = 0.1, 0.4, 0.8, 1.2, and 1.6 km [0.06, 0.25, 0.5, 0.75, 1.0 mi]) 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 with 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 0.8 km (0.5 mi) of nest or roost sites and decreased at increasing spatial scales (Grubb et al. 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 0.1 km (0.06 mi) of owl nests, where the >70% canopy-cover class was most abundant.

Peery et al. (1999) evaluated the use of specific cover types by Mexican spotted owls in the Tularosa Mountains, New Mexico, and the spatial configuration of those cover types. This study area was dominated by mixed-conifer forest (Peery et al. 1999: Table 1). 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 500 m (1,640 ft) (area = 78.9 ha [195 ac]) to 4,000 m (13,123 ft) (area = 5,030 ha [12,429 ac]). These circles thus 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 Peery et al. (1999), areas around Mexican spotted owl nest and roost sites contained greater amounts of both mature mixed-conifer forest and mature ponderosa pine (Pinus ponderosa) forest than random sites. Differences between owl and random sites persisted across all spatial scales but were most pronounced within 500 m (1,640 ft) of the nest or roost and declined with increasing spatial scale (Peery et al. 1999: Figs. 1 and 2). Visual inspection of Figures 1 and 2 in Peery et al. (1999) suggests that much of the difference in vegetation composition at larger scales was driven by differences at smaller scales (i.e., to inclusion of area sampled by smaller circles in larger 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 a study area dominated by ponderosa pine - Gambel oak (Quercus gambelii) forest in the Coconino National Forest, Arizona (this area was included in the study area in Grubb et al. [1997]). They compared 51 owl nest or roost sites with an equal sample of random sites at three spatial scales: a circular plot of 800-m (2,625-ft) radius (area = 201 ha [497 ac]), and two 400-m (1,312-ft) wide “ring” plots between 800 m (2,625 ft) and 1600 m (5,249 ft) 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 May and Gutiérrez (2002) differed between owl and random sites only within the 201-ha analysis area. Areas around owl nest and roost sites contained more mature mixed-conifer forest and young mixed-conifer forest with canopy cover >55% than expected based on availability. Young forests were used only where residual large (>45.7 cm [18 in] diameter at breast height [dbh]) trees were present. 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).

In summary, current studies of landscape composition suggest that owls locate home ranges non-randomly, placing them in areas such that the center of the home range contains greater than
average amounts of mature forest or in areas of younger forest with high canopy cover and containing residual large trees. Differences in landscape composition between owl and random sites generally were greatest near nest or roost sites and decreased with increasing area. This may indicate that owls are most selective for nesting or roosting core areas, or simply that larger circular analysis areas included more unused habitat or habitat used primarily for foraging. In general, the scale at which differences between owl and random sites were most pronounced (201 ha [497 ac]; Grubb et al. 1997, May and Gutiérrez 2002) correlated reasonably well with the size of Protected Activity Centers (PACs; 243 ha [600 ac]) recommended in USDI FWS (1995) and in this Recovery Plan.

B. Home Range Scale

a. Space Use.—Four concepts are relevant to understanding space and habitat use by resident Mexican spotted owls: territory, home range, activity center, and core area. A territory is defined as an exclusive area defended by the occupant (Welty 1975:224-225). A home range is defined as the area used (but not always defended) by an animal during its normal activities (Burt 1943). Unlike territories, home ranges of adjacent pairs may overlap spatially. Home ranges more appropriately define the area from which all resources required for a given time period are obtained by an organism. An activity center is an area within the home range receiving concentrated use. The activity center could be the same size as a territory when the former is small and consistently defended. 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, Reynolds et al. 1992, Ward and Salas 2000). Activity centers and core-areas have been used to estimate the size of areas needed to protect habitat most commonly used by spotted owls (e.g., Bingham and Noon 1992, Gutiérrez et al. 1992, USDI FWS 1995).

Spotted owls are described as territorial in that mated pairs defend a breeding territory, at least during the nesting season. Fidelity to these territories is apparently high in Mexican spotted owls, with many owls remaining on the same territory year after year (Gutiérrez et al. 1995). No direct estimates of territory size are available for Mexican spotted owls. However, estimates of nearest-neighbor distances between adjacent pairs may provide some 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. One of these study areas was located in the Tularosa Mountains, New Mexico (Peery et al. 1999) and the other in north-central Arizona (May and Gutiérrez 2002). Mean distances between adjacent pairs in these areas were 2.1 km (1.3 mi) in New Mexico ($n = 31$ pairs) and 2.4 km (1.5 mi) in Arizona ($n = 42$ pairs), suggesting that exclusive use areas average approximately 346 to 452 ha (855 to 1,115 ac), respectively.

Investigators have studied home-range size of Mexican spotted owls directly by monitoring movements of radio-marked owls in a number of different geographic areas and/or habitats (Table B.2). Home-range size appears to vary considerably both among these studies (Table B.3) and between the breeding and non-breeding seasons. The factors underlying variation among studies are unclear, however. For example, various studies used different sampling
Table B.2. Characteristics of study areas where movements of radio-marked Mexican spotted owls were monitored (from Ganey and Block 2005a).

<table>
<thead>
<tr>
<th>Study area</th>
<th>State</th>
<th>General landform</th>
<th>Primary cover types¹</th>
<th>Source²</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Francisco Peaks</td>
<td>Arizona</td>
<td>Montane slopes</td>
<td>Mixed-conifer, ponderosa pine</td>
<td>1</td>
</tr>
<tr>
<td>Walnut Canyon</td>
<td>Arizona</td>
<td>Incised canyon</td>
<td>Mixed-conifer, ponderosa pine, riparian, ponderosa pine/pinyon-juniper/oak</td>
<td>1</td>
</tr>
<tr>
<td>Sacramento Mountains³</td>
<td>New Mexico</td>
<td>Montane slopes and canyons</td>
<td>Mixed-conifer, ponderosa pine, pinyon-juniper</td>
<td>2, 3</td>
</tr>
<tr>
<td>Sacramento Mtns – mesic³</td>
<td>New Mexico</td>
<td>Montane slopes and canyons</td>
<td>Mixed-conifer, ponderosa pine, pinyon-juniper</td>
<td>4</td>
</tr>
<tr>
<td>Sacramento Mtns. – xeric³</td>
<td>New Mexico</td>
<td>Montane slopes and canyons</td>
<td>Mixed-conifer, ponderosa pine, pinyon-juniper</td>
<td>4</td>
</tr>
<tr>
<td>Bar-M Canyon</td>
<td>Arizona</td>
<td>Rolling hills, cinder Cones</td>
<td>Ponderosa pine – Gambel oak, ponderosa pine</td>
<td>5</td>
</tr>
<tr>
<td>Colorado</td>
<td>Colorado</td>
<td>Incised canyons</td>
<td>Mixed-conifer, pinyon-juniper, Ponderosa pine</td>
<td>6</td>
</tr>
<tr>
<td>Southern Utah</td>
<td>Utah</td>
<td>Incised canyons</td>
<td>Pinyon–juniper, mixed-conifer</td>
<td>7</td>
</tr>
<tr>
<td>Grand Canyon</td>
<td>AZ</td>
<td>Incised canyon</td>
<td>Pinyon-juniper</td>
<td>8</td>
</tr>
</tbody>
</table>


² Sources: 1 = Ganey and Balda 1989b (UGM EMU); 2 = Zwank et al. 1994 (BRE EMU); 3 = Skaggs 1990 (BRE EMU); 4 = Ganey et al. 2005 (BRE EMU); 5 = Ganey et al. 1999 (UGM EMU); 6 = Johnson 1997 (Southern Rocky Mountains [SRM] EMU); 7 = Willey and van Riper 2000, 2007 (CP EMU); 8 = Bowden 2008 (Grand Canyon National Park, CP EMU).

³ Ganey et al. (2005) recognized two distinct study areas in the Sacramento Mountains, whereas Zwank et al. (1994) and Skaggs (1990) did not. The mesic area was dominated by mixed-conifer forest, the xeric area by drier forest and woodland types.
Table B.3. Size (ha) of home ranges or activity centers (where available) of radio-marked Mexican spotted owls during the breeding and non-breeding seasons, as estimated in various studies. Seasons followed Ganey and Balda (1989b) in all studies (breeding season = 1 Mar – 30 Aug). \(N\) = number of owls included in estimates. Home range estimates based on the minimum convex polygon estimator (Zwank et al. 1994) or 95% adaptive kernel estimator (Ganey et al. 1999, 2005; Willey and van Riper 2007, Bowden 2008). Activity centers based on the 75% adaptive kernel estimator.

<table>
<thead>
<tr>
<th>Parameter / Study area</th>
<th>Breeding season</th>
<th>Non-breeding season</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N)</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td><strong>Home-range size /</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sacramento Mountains(^1)</td>
<td>9</td>
<td>278</td>
<td>75.3(^2)</td>
</tr>
<tr>
<td>Sacramento Mtns. – mesic(^1)</td>
<td>6</td>
<td>228.1</td>
<td>37.3</td>
</tr>
<tr>
<td>Sacramento Mtns. – xeric(^1)</td>
<td>6</td>
<td>458.9</td>
<td>83.4</td>
</tr>
<tr>
<td>Bar-M Canyon</td>
<td>8</td>
<td>392.5</td>
<td>70.0</td>
</tr>
<tr>
<td>Southern Utah</td>
<td>12</td>
<td>545</td>
<td>518(^5)</td>
</tr>
<tr>
<td>Grand Canyon</td>
<td>5</td>
<td>562</td>
<td>84</td>
</tr>
<tr>
<td><strong>Activity-center size /</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sacramento Mtns. – mesic(^1)</td>
<td>6</td>
<td>69.9</td>
<td>9.5</td>
</tr>
<tr>
<td>Sacramento Mtns. – xeric(^1)</td>
<td>6</td>
<td>156.2</td>
<td>22.0</td>
</tr>
<tr>
<td>Bar-M Canyon</td>
<td>8</td>
<td>121.7</td>
<td>21.8</td>
</tr>
</tbody>
</table>

\(^1\) Zwank et al. (1994) pooled owls within the Sacramento Mountains when estimating size of seasonal home ranges, whereas Ganey et al. (2005) recognized two distinct study areas in the Sacramento Mountains. The mesic area was dominated by mixed-conifer forest, the xeric area by drier forest and woodland types.

\(^2\) \(SE\) estimated from data in Zwank et al. (1994)

\(^3\) Results presented here were recalculated using data from the sample of owls discussed in Ganey et al. (2005). Ganey et al. (2005) did not present data on activity-center size, and summarized data on home-range size in a figure.

\(^4\) 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.

\(^5\) Standard deviation (Willey and van Riper 2007).
methods or home-range estimators, and studies were conducted in different years. All of these factors can influence estimates of home-range size (Kernohan et al. 2001), making direct comparisons among studies difficult. Consequently, observed differences among studies could be due to differences in methods, local habitat quality including abundance of prey, biogeographic effects (e.g., differences in climate pattern or biogeographic region), temporal variation (studies conducted in different years), or all of the above.

A study that used consistent methods simultaneously across two study areas in the Sacramento Mountains, New Mexico, suggested that differences in local habitat quantity and/or quality influenced home-range size (Ganey et al. 2005). Home-range size was greater during both the breeding and non-breeding seasons in a study area dominated by xeric forest types than in a study area dominated by mesic mixed-conifer forest (Tables B.2 and B.3). Further, range size was inversely related to the proportion of the home range consisting of mixed-conifer forest. This relationship held both within study areas and across both study areas considered together, and in both seasons (Ganey et al. 2005). Owls roosted primarily in mixed-conifer forest in both study areas, and observed fecundity and survival rates of radio-marked owls were lower in the area dominated by xeric forests than in the area dominated by mixed-conifer forest (Ganey et al. 2005). Collectively, these observed patterns suggested that differences in local habitat quality helped explain the variation in home-range size.

Some investigators also estimated size of seasonal activity centers (Table B.3). Again, considerable variability was observed across studies. In general, however, activity centers were considerably smaller than home ranges of radio-marked owls. Noting this concentration of activity in a portion of the home range, the recommended size of PACs in USDI FWS (1995) and in this Recovery Plan was based on activity centers rather than home ranges, in an attempt to focus management on the areas most used by the owls.

Thus, 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 methods among studies, but we assume that some of the observed variation is real. At this time, the relative influences of biogeographic regions versus local differences in habitat quality on home-range size of Mexican spotted owls remain unclear, although limited information suggests that such local differences may be important (Ganey et al. 2005, see also Carey et al. 1992, Zabel et al. 1995).

b. Habitat Use Within the Home Range.—Within their home range, Mexican spotted owls nest, roost, forage, and disperse in a diverse array of biotic communities. They can be found in heavily forested areas as well as in rocky canyons with sparse or no forest cover (Ligon 1926, Ganey and Dick 1995, Ward et al. 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 for use 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. The Sacramento Mountains of south-central New Mexico provide a good example of forest-dwelling Mexican spotted owls. There, owls occur in heavily forested
mountains and typically are not closely associated with rock outcrops or cliffs (Ganey et al. 2000, Ward 2001, Lavier 2006). In contrast, Mexican spotted owls in the canyonlands of southern Utah and northern Arizona (e.g., Zion, Canyonlands, Capitol Reef, and Grand Canyon National Parks) occur in narrow slickrock canyons, are closely associated with cliff-forming rock formations, and are not reliant on extensive forest cover (Kertell 1977, Rinkevich and Gutiérrez 1996, Willey 1998b, Willey and van Riper 1998, 2007, Willey and Ward 2004, Bowden 2008).

Throughout their range, Mexican spotted owls are often, but not always, associated with steep topography (Ganey and Dick 1995). This association is particularly prominent in the canyonlands, where the topography likely contributes directly to habitat suitability. Owls in these areas frequently nest and roost on ledges on steep cliffs, or in caves, potholes, or alcoves formed in these cliffs (e.g., Rinkevich and Gutiérrez 1996, Willey and van Riper 1998, Willey and Ward 2004, Bowden 2008, Mullet 2008, see also Johnson 1997). These types of structures tend to occur most frequently in the same formations where deep, narrow, complex canyon systems with exposed cliffs are formed (see Box B.1 for a fuller discussion of Habitat of Canyon-dwelling Owls).

In more heavily forested areas, the reasons underlying the frequent association between owls and steep topography are less clear. Owls in these areas typically inhabit mature forests, and in many cases these forests are restricted to steep topography due to past harvest of forests elsewhere (Ganey and Balda 1989a, Ganey and Benoit 2002). In at least some areas, however, owls occur in gentle terrain where suitable forest structure is present (Ganey et al. 1999, 2000). This suggests that the association between owls and steep terrain in forested areas may be driven more by the influence of forest structure than by topography itself. However, diverse topography also contributes to diversity in vegetation types and structure in the southwest. This diversity in turn contributes to habitat complexity, a feature that seems to be common to areas occupied by Mexican spotted owls (Ganey and Balda 1989a, Willey and van Riper 1998, Willey and Ward 2004). Areas of diverse topography, especially where significant rock outcrops or cliffs are present, also may serve as fire refugia (Camp et al. 1997), reducing the frequency of widespread surface fires and allowing longer periods for development of forest structure. Regardless of the underlying mechanism, the association between owl occupancy and steep terrain is strong, even in forested terrain (see Bowden et al. 2003, Ganey et al. 2004). Indeed, this association is strong enough that several investigators have based predictive models of owl habitat primarily on topographic features (see Habitat Models).

In both forest and canyon environments, Mexican spotted owls tend to select roosting and nesting sites that provide thermal protection. In the case of forested sites, large trees, dense canopy cover, and first or second order tributaries all act to create a cooler microclimate during warm ambient temperatures of the breeding season (e.g., Ward and Salas 2000, Ganey 2004).

c. **Cover Types.**—Use of cover types by Mexican spotted owls varies according to geographic region. Much of this regional variation likely reflects regional variation in habitat composition, climate pattern, and prey availability.
BOX B.1
HABITAT OF CANYON-DWELLING MEXICAN SPOTTED OWLS

In parts of its range, the Mexican spotted owl occupies a variety of steep, rocky-canyon habitats (Kertell 1977, Ganey and Balda 1989a, Rinkevich and Gutiérrez 1996, Willey 1998b, Willey and Ward 2004, Willey and van Riper 2007, Bowden 2008, Mullet 2008). A complex of physical gradients (including water availability, amount of sunlight, slope, and elevation) can produce a “canyon effect” (Dick-Peddie 1993). The physical shape and dimension of canyons can affect local temperature, humidity, and vegetation, enhancing key welfare factors (e.g., nest and roost habitats) for the owl, particularly within arid portions of its range (Barrows 1981, Rinkevich and Gutiérrez 1996, Willey 1998b). Rocky cliffs and canyon rims can modify the amount of direct sunlight penetrating inner-canyon habitats, so that vegetation communities and microclimates may vary greatly among topographic zones (e.g., washes, benchlands, talus slopes, cliffs, and rim habitats). Canyon walls also can create complex habitat structure, a feature typically associated with habitats used by forest-dwelling spotted owls (Forsman et al. 1984, Ganey and Dick 1995).

Rocky canyon habitats used by Mexican spotted owls typically include dendritic watersheds with myriad tributary canyons, a variety of vegetation communities (ranging from arid to mesic), and prominent vertical-walled or overhanging cliffs (Rinkevich and Gutiérrez 1996, Willey 1998b, Swarthout and Steidl 2001). Within canyon habitats, Mexican spotted owls may nest and roost on cliff faces using protected caves or ledges (Rinkevich and Gutiérrez 1996, Willey 1998b, Bowden 2008) or roost in small patches of riparian tree species (Bowden 2008, Mullet 2008), and forage among caves, cliff faces, and rim or canyon-bottom vegetation for various small mammals, including mice (Peromyscus spp.), woodrats (Neotoma spp.), and bats (Vespertilionidae) (Ganey 1992, Ward and Block 1995, Rinkevich and Gutiérrez 1996, Willey 1998b, Johnson 1997, Sorrentino and Ward 2003).

We recognize several broad patterns of habitat use by Mexican spotted owls that occupy rocky-canyon habitats:

- Mexican spotted owl home ranges include a significant component of vertical walled rocky canyons with numerous cliffs, caves, ledges, and branching tributary canyons. Mexican spotted owls use nest, roost, and foraging habitats that are strongly associated with complex vertical and horizontal landscape structure, complex geomorphology, and canyon- and cliff-forming geologic substrates. Rocky architecture (e.g., slope, aspect, and ruggedness) may provide important habitat components (e.g., nest sites, roost sites, shade, foraging surfaces) normally associated with forest vegetation structure.

- Home ranges and activity centers used by Mexican spotted owls in canyon habitat can include a diversity of vegetation types, including desert-scrub, pinyon (Pinus spp.) –juniper (Juniperus spp.) woodland, riparian, ponderosa pine-oak, and mixed-conifer forest. Therefore it may be difficult to rely on vegetation alone to identify suitable habitat.

- Mexican spotted owls in canyon habitats primarily use rugged terrain located below canyon rims, and all known breeding sites and associated nesting cores areas have been located below the canyon rims (Willey and van Riper 2007, Bowden 2008). However, home-range data in some areas also indicate that the owls may use rims and mesa tops when hunting and vocalizing (Willey and van Riper 2007, Bowden 2008). Thus, adjacent highlands should not be ignored in management planning.

Canyon habitats occupied by Mexican spotted owls possess some common emergent properties. These primary elements include rocky cliffs, parallel-walled canyons, relatively long canyon complexes, cool north-facing aspects, complex branched tributary side-canyons, and a mosaic of vegetation communities ranging from cool riparian through montane forest to arid scrub desert. There are exceptions to these emergent properties, however, including occasional use of small side canyons and areas not on north-facing aspects.
In the northern portion of the Mexican spotted owl's range, including Utah, Colorado, and parts of far northern Arizona and New Mexico (CP and SRM EMUs), owls occur primarily in steep-walled, rocky canyons (Kertell 1977, Rinkevich and Gutiérrez 1996, Johnson 1997, Willey and van Riper 1998, Willey and Ward 2004, Bowden 2008). These canyon systems vary in the amount of forest cover present, but in general they are less heavily forested than are canyons occupied farther south. Pinyon-juniper woodlands and mixed-conifer forest are prominent cover types used in these canyon systems (Ganey and Dick 1995, Willey 1998b), but in some cases these canyons are entirely or largely lacking forest or woodland cover.

Farther south, a wider range of cover types are used. For example, along the Mogollon Rim in Arizona and New Mexico (UGM EMU), spotted owls occur in mixed-conifer forests, ponderosa pine-Gambel oak forests, and associated riparian forests (Ganey and Balda 1989a, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Peery et al. 1999, Stacey and Hodgson 1999, May and Gutiérrez 2002, Stacey 2010). They frequently occur in canyon systems and in association with steep terrain in this region as well. These canyons generally have greater forest cover than canyons in the northern portion of the range, however, and owls are not restricted to canyons and steep terrain in this region.

South of the Mogollon Rim, in southern New Mexico, and into Mexico (BRE, BRW, and Mexican EMUs) an even wider range of cover types are used, including mixed-conifer, Madrean pine-oak, and Arizona cypress (Cupressus arizonica) forests, encinal oak woodlands, and associated riparian forests (e.g., Ganey and Dick 1995, Tarango et al. 1997, 2001, Young et al. 1998, Márquez-Olivas et al. 2002, Mullet 2008, Mullet and Ward 2010). Some owls are found in association with canyon systems or steep montane terrain. But, as along the Mogollon Rim, many of these canyons contain extensive forest or woodland cover, and owls are not restricted to deep rocky canyons except for small populations of owls occurring in southern portions of the BRE EMU (e.g., Guadalupe and Davis Mountains, Mullet 2008). Thus, there appears to be a north-south gradient in diversity of habitats used, with a wider range of both cover types and terrain types used in the southern portion of the range than in the northern portion (Ganey and Dick 1995).

Despite the diversity of cover types where Mexican spotted owls have been found, these owls most commonly use mixed-conifer forests throughout their range within the U.S. (e.g., Ganey and Dick 1995, Seamans and Gutiérrez 1995, Willey 1998a, Stacey and Hodgson 1999, Ganey et al. 2000, Ward 2001, Stacey 2010). These forests are dominated by Douglas-fir (Pseudotsuga menziesii) and/or white fir (Abies concolor), with co-dominant species including southwestern white pine (P. strobiformis), limber pine (P. flexilis), and ponderosa pine (Brown et al. 1980). The understory often contains the above coniferous species as well as broadleaved species such as Gambel’s oak, maples (Acer spp.), box elder (A. negundo), and New Mexico locust (Robinia neomexicana). These broadleaved species may be important (Ganey et al. 1992, 1999, 2003, Seamans and Gutiérrez 1995, Stacey and Hodgson 1999, May and Gutiérrez 2002, May et al. 2004), either in adding to structural complexity or by providing nest sites (SWCA 1992, Fletcher and Hollis 1994, May and Gutiérrez 2002, May et al. 2004) or additional food sources for prey species (Ward 2001).

Madrean pine-oak forests used by Mexican spotted owls are dominated by an overstory of various pine species in conjunction with species such as Douglas-fir and Arizona cypress. In
southern Arizona, pine species represented include primarily Apache (P. engelmannii), Chihuahuan (P. leiophylla), and Arizona (P. arizonica) pine. Farther south, a number of other pine species are present. For example, a study area in the state of Chihuahua, Mexico, included the pines discussed above as well as Durango (P. durangensis), Mexican white (P. ayacahuite), and weeping (P. patula) pine (Tarango et al. 1997). Still farther south, in Aguascalientes, Apache and Arizona pines dropped out, whereas ocote (P. oocarpa), nut (P. cembroides), and Michoacán (P. michoacana) pine were present (Tarango et al. 2001, Márquez-Olivas et al. 2002). Evergreen oaks were prominent in the understory in all of these pine-oak types (Brown et al. 1980, Tarango et al. 1997, 2001, Young et al. 1998, Márquez-Olivas et al. 2002).

In areas where Mexican spotted owls inhabit canyons, canyon structure and cover types can vary according to geographic region. The following sections provide separate canyon habitat descriptions for the CP, New Mexico portion of SRM, and BRE EMUs.

1. **CP EMU.**—In Utah, the type of incised canyon habitat occupied by Mexican spotted owls is present in Dinosaur National Monument, Desolation Canyon, the San Rafael Swell, Zion National Park, Grand Staircase-Escalante National Monument, Glen Canyon National Recreation Area, Capitol Reef National Park, and Canyonlands National Park. Canyon habitat also occurs in the Dixie, Manti LaSal, and Fishlake National Forests and on large tracts of land managed by the BLM. In Colorado, examples of rocky canyon habitat occur in and around Mesa Verde National Park and on Ute Tribal Lands. In Arizona, similar canyon habitat is present on the Navajo Nation, in Grand Canyon National Park, and on BLM – administered lands (e.g., Paria Canyon).

Willey (1998a, see also Willey and van Riper 2007) studied movements and habitat associations of radio-marked Mexican spotted owls in canyon habitat in southern Utah. Radio-marked owls inhabited areas featuring steep cliffs, rocky topography, and canyons with complex vertical and horizontal structure (Willey 1998b). They typically used roost sites characterized by cool daytime temperatures (relative to nearby randomly located sites) and relatively high overhead cover provided by canyon walls and vegetation (Willey 1998b: Table 4-2). Many roost sites had large conifers or deciduous trees nearby, but others were in areas dominated by pinyon-juniper woodland or desert-scrub vegetation (Rinkevich and Gutiérrez 1996, Johnson 1997, Willey 1998b). Tall cliffs and/or small stands of mixed-conifer forest provide the owls with cool microsites for roosts and nests. Although pinyon-juniper woodland was the most common vegetation type present in owl home ranges in Utah and in the Grand Canyon (Bowden 2008), mixed conifer forest, including Douglas-fir and white fir, was present within one-third of habitat plots randomly located within owl home ranges (Willey 1998b). Eighty-eight percent of telemetry locations occurred below the canyon rims (Willey and van Riper 2007). Thus, suitable canyon habitat can include canyon, rim, and adjacent mesa and plateau landscapes (see also Bowden 2008).

2. **SRM EMU.**—Within this EMU, Mexican spotted owls occur across a wide elevational gradient and occur in both forested mountains and canyons (Johnson and Johnson 1985, Johnson 1997, Hathcock and Haarmann 2008). Owls are more likely to be found in rocky canyons toward the lower end of their elevational range in this region, and more likely to inhabit forests at higher elevations (where forest cover tends to be more continuous on the landscape; T. Johnson, pers. comm.). For example, many owls occur in rocky canyons
incised into volcanic-tuff at lower elevations in the Jemez Mountain Range in northern New Mexico (Santa Fe National Forest and Bandelier National Monument; Johnson and Johnson 1985). These canyons provide many potholes, ledges, and small caves for owls to use for roosting and nesting (Johnson and Johnson 1985). Owls at higher elevations, both in the Jemez and Sangre de Cristo Mountains, are less restricted to rocky canyon situations but generally still occur in areas characterized by high topographic relief. Even at higher sites in the Jemez Mountains, however, many owls nest in cavities in small outcrops of tuff (T. Johnson, pers. comm.).

Vegetation in canyon bottoms and on canyon slopes includes species typical of mixed-conifer forest, such as Douglas-fir, white fir, and ponderosa pine. Deciduous species such as cottonwoods (Populus spp.), Gambel oak, boxelder, and alder (Alnus spp.) also are present in canyon bottoms (Johnson and Johnson 1985, Johnson 1997). Patches of pinyon-juniper and aspen (P. tremuloides) also occur within these canyons. At higher elevations, common species include Engelmann spruce (Picea engelmannii), subalpine fir (A. lasiocarpa), blue spruce (P. pungens), and limber pine (Hathcock and Haarmann 2008). As in many areas in the northern portion of the owls’ range, high-elevation forests appear to contain greater amounts of spruce, true firs, and aspen than the mixed-conifer forests occupied by owls farther south.

3. BRE EMU.—Mexican spotted owls in this EMU occur in both forests and rocky canyons. For example, owls are abundant in mixed-conifer forests within the Sacramento Mountains, but they also have been found in the rocky-canyon networks of the Guadalupe and Davis Mountains in southern New Mexico and West Texas, as well as in Carlsbad Caverns National Park, New Mexico. These canyons contain riparian vegetation and encinal woodlands (Brown et al. 1980). In the latter cover type the dominant non-coniferous trees are evergreens, especially oaks and Texas madrone (Arbutus xalapensis). Coniferous trees such as pinyon pine (P. edulis), junipers, and ponderosa pine occur in low to moderate densities. Owls in these canyons roost in caves, cliff crevices, or in trees associated with springs or riparian corridors (Bryan and Karges 2001, Mullet 2008). In the Guadalupe Mountains, nest and roost sites occurred in steep, mesic canyons containing bigtooth maple (A. grandidentatum), western hop-hornbeam (Ostrya knowltonii), Chinkapin oak (Q. muehlenbergii), Douglas-fir, southwestern white pine, and Gambel oak (Mullet 2008, Mullet and Ward 2010).

d. Space Use of Resident Owls During the Non-breeding Season.—Resident Mexican spotted owls expanded their home range during the non-breeding season in all areas where seasonal home range estimates were available, although the magnitude of this seasonal expansion varied among areas (Table B.3). Clearly, owl home ranges were larger than PACs as defined in USDI FWS (1995:84-89). But PAC size was based on the size of owl activity centers, not home ranges. Size of owl activity centers was more comparable to PAC size in the three study areas where estimates were available (Table B.3). Spatial overlap between seasonal activity centers was considerable (Table B.4). In general, non-breeding-season activity centers contained most of the breeding-season activity center. The mean proportion of the non-breeding-season activity center contained in the breeding-season activity center was lower but still indicated considerable
Table B.4. Spatial overlap between seasonal activity centers (AC; estimated as the 75% adaptive kernel contour) of radio-marked Mexican spotted owls in three study areas\(^1\). \(N\) = number of owls included in estimate; only owls with valid range estimates during both the breeding and non-breeding seasons were included in estimates (from Ganey and Block [2005]).

<table>
<thead>
<tr>
<th>Study area</th>
<th>N</th>
<th>Mean (Mean SE)</th>
<th>Observed (Mean SE)</th>
<th>Maximum (Mean SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sacramento Mtns.–mesic</td>
<td>6</td>
<td>85.7 (4.6)</td>
<td>66.9 (5.6)</td>
<td>82.6 (8.4)</td>
</tr>
<tr>
<td>Sacramento Mtns.–xeric</td>
<td>6</td>
<td>78.0 (7.1)</td>
<td>48.8 (6.7)</td>
<td>65.4 (14.0)</td>
</tr>
<tr>
<td>Bar-M Canyon</td>
<td>8</td>
<td>91.4 (3.1)</td>
<td>35.5 (9.0)</td>
<td>42.6 (13.0)</td>
</tr>
</tbody>
</table>

\(^1\) Based on data from a sample of radio-marked owls included in Ganey et al. (1999, 2005). The parameters estimated here were not included in previous papers.

\(^2\) Theoretical maximum proportion of the non-breeding-season activity center that could be contained in a breeding-season activity center given observed size of those breeding-season activity centers, assuming maximum spatial overlap.
spatial overlap. Further, the smaller size of breeding-season activity centers relative to non-breeding-season activity centers effectively limits the possible range for this measure of overlap (Table B.4). Thus, protection of nesting areas provides protection to areas used by resident owls throughout the year, not only during the breeding season.

e. Habitat Use by Resident Owls During the Non-breeding Season.—Little detailed information is available on habitat use by resident owls during the non-breeding season, but there is some evidence for use of more open habitats at this time. For example, Zwank et al. (1994) reported that owls in the Sacramento Mountains roosted in “shorter trees with less dense foliage” during the winter. Willey (1998a:73) reported that “during winter… Mexican spotted owls were observed roosting in more open habitats.” In contrast to this trend, however, he also reported that some owls moved out of steep slickrock canyon terrain and into forested uplands during winter. Johnson (1997:49) noted that wintering owls used “…canyons with a north-south orientation dominated by pinyon-juniper woodlands with scattered patches of ponderosa pine.” This latter description included owls classified as both residents and migrants by Ganey and Block (2005a; see also Seasonal Migration section).

In a study of radio-marked owls in pine-oak forests of north-central Arizona, relative areas of cover types did not differ between seasonal home ranges, but relative area in canopy-cover classes did (Ganey et al. 1999). Relative to non-breeding-season ranges, breeding-season ranges contained more area with canopy cover ≥60% and less area with canopy cover ranging from 20 to 39%. Structural features of forest stands used by foraging owls did not differ between seasons, but structure of stands used by roosting owls did. Stands used for roosting during the breeding season had greater live-tree basal area, oak basal area, and canopy cover than stands used during the non-breeding season (Ganey et al. 1999: Table 5). In an analysis focused on a finer spatial scale, canopy cover surrounding roost “microsites” also was greater during the breeding than the non-breeding season in this area (Ganey et al. 2000).

Ganey et al. (2000, 2003) also reported on aspects of habitat use by radio-marked owls in the Sacramento Mountains at these same spatial scales (stand and roost microsite). They found little evidence for differences in seasonal habitat use at either scale within the Sacramento Mountains, for either foraging or roosting use.

In summary, there is evidence for shifts in habitat use in some areas, but not in others. In general, evidence for seasonal differences in habitat use appears strongest where owls occupy rocky canyons in the northern portion of their range. In mixed-conifer forests farther south, seasonal differences in habitat use were less pronounced, and patterns were intermediate in an area where owls occupied pine-oak forest. Where resident owls do use different habitats during the winter, available evidence suggests that those habitats generally are more open in structure.

C. Microhabitat Features

a. Nests and Roosts.—Mexican spotted owls nest and roost primarily in closed-canopy forests or rocky canyons. In the northern portion of the range (southern Utah, Colorado, and parts of northern Arizona and northern New Mexico) and extreme southeastern portions of the range (Mullet 2008), most nests are in caves or on cliff ledges in steep-walled canyons (Johnson 1997,
Elsewhere, the majority of nests appear to be in trees (Fletcher and Hollis 1994, Seamans and Gutiérrez 1995, May and Gutiérrez 2002, May et al. 2004), but cliffs and caves can be locally important (e.g., Bryan and Karges 2001, Márquez-Olivas et al. 2002).


Tree species used for nesting vary somewhat among areas and habitat types. Douglas-fir is the most common species of nest tree in many areas, particularly areas dominated by mixed-conifer forest (SWCA 1992, Fletcher and Hollis 1994, Seamans and Gutiérrez 1995, Johnson 1997). In pine-oak forests where nesting has been studied in the U.S., nests were commonly found in cavities in large oak trees, followed by platforms in ponderosa pine trees (Ganey et al. 1992, SWCA 1992, Fletcher and Hollis 1994, May and Gutiérrez 2002, May et al. 2004). Only one nest has been reported from Mexican pine-oak forest. This nest was in a 30-cm (12-in) dbh Mexican white oak tree (Q. polymorpha, nest structure type not reported; Tarango et al. 1997).

A wider variety of trees are used for roosting, but patterns again vary among forest types and geographic regions. As for nesting, Douglas-fir is the most commonly used species in many areas dominated by mixed-conifer forest (Ganey 1988, Fletcher and Hollis 1994, Zwank et al. 1994, Johnson 1997, Stacey and Hodgson 1999, Ganey et al. 2000). In contrast, owls roost primarily in oaks and pines in areas dominated by pine-oak forests (Ganey et al. 1992, Young et al. 1997, Ganey et al. 2000, Tarango et al. 2001, May et al. 2004, Márquez-Olivas et al. 2002). The most frequently occurring tree species at roost sites in canyons in south-eastern New Mexico
and West Texas are bigtooth maple, western hop hornbeam, and chinkapin oak (Mullet and Ward 2010).

b. Foraging.—Most studies of foraging habitat are based on triangulated locations of radio-marked owls, because it is impossible to visually observe foraging behavior of wide-ranging owls at night. Triangulated locations are inherently inaccurate in the types of terrain and forests occupied by Mexican spotted owls (e.g., Ganey et al. 2003). As a result, our understanding of habitat use by foraging owls is limited. Available studies suggest considerable variability in use of foraging habitat, however, both among study areas and among individuals within study areas (Ganey and Balda 1994, Hodgson 1996, Willey 1998b, Ganey et al. 1999, 2003).

Owls in the canyonlands of southern Utah apparently forage primarily in rocky canyons, as 88% of locations of radio-marked owls fell within canyons (Willey and van Riper 2007, Bowden 2008). Specific features of foraging habitats were not reported in these studies. Owls in most forested study areas show some selectivity for foraging habitat relative to randomly available habitat, but the level of selectivity is reduced relative to habitat-use patterns for roosting and nesting. For example, owls typically forage in all forest stands used for roosting but do not roost in all stands in which they forage (Ganey et al. 1999, 2003). Areas used for foraging typically were in closed-canopy forests featuring high basal area of trees and high volume of logs (Ganey and Balda 1994, Ganey et al. 1999, 2003). Structural characteristics of areas used for foraging differed from those of proximal but random areas in some study areas (Ganey and Balda 1994, Hodgson 1996, Ganey et al. 1999) but were more variable than characteristics of stands used for roosting in all areas (Ganey and Balda 1994, Hodgson 1996, Ganey et al. 1999, 2003). Additional information on variability of the owl’s foraging habitat also can be inferred from microhabitat descriptions for the owl’s common prey (see Prey Ecology).

D. Summary of Habitat Use

Most studies of how Mexican spotted owls use their habitat have sampled habitat characteristics or otherwise quantified habitat use at relatively fine scales (<0.2 ha [0.5 ac], reviewed in Ganey and Dick 1995). As a result, we know relatively little about patterns of habitat use at coarser scales, including structure of forest stands and landscape composition (but see Grubb et al. 1997, Ganey et al. 1999, 2003, Peery et al. 1999, May and Gutiérrez 2002).

Patterns of habitat use vary with owl activity, seasonally, and regionally. For example, owls appear to be far more selective for habitats used for roosting and nesting than for habitats used for foraging (Ganey and Balda 1994, Ganey et al. 1999, 2003). Within areas that contain suitable roosting and nesting habitat, owls forage in a broader array of both cover types and structural conditions (Ganey and Balda 1994, Ganey et al. 1999, 2003). Similarly, selection for particular types of habitats appears to be relaxed during the non-breeding season, when owls wander more widely and use a wider array of habitats that also tend to have a more open structure. Based on these findings, USDI FWS (1995) explicitly assumed that the presence of suitable habitat for roosting and nesting limited distribution of Mexican spotted owls and primarily based management recommendations on retaining and enhancing such habitat.
a. Reasons Underlying Habitat-Use Patterns.—There are several possible mechanisms underlying 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 protection 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 habitat gradient that is occupied. 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 (e.g., Ganey and Dick 1995, Seamans and Gutiérrez 1995, Grubb et al. 1997, Willey 1998b, Ganey et al. 1999, 2000, Willey and Ward 2004).

There is empirical evidence in support of this hypothesis in addition to observed patterns of habitat use. Ganey et al. (1993) observed that Mexican spotted owls produced more metabolic heat than great horned owls and were less able to dissipate that heat through evaporative cooling. Teng (1998) compared thermal environments of northern spotted owl roost and random sites in interior forests in northwestern California and estimated that roosting in randomly sampled areas would increase energy costs for thermoregulation by 5 to 34% per day and evaporative water loss by up to 5% per day relative to the sampled roost sites. Weathers et al. (2001) studied metabolic rate and water flux of California spotted owls in the field using doubly-labeled water. They determined that rates of water flux were high relative to metabolic rates and suggested that minimizing water loss might contribute to the owls’ preference for cooler environments. Ganey (2004) sampled thermal environments throughout most of the breeding season (May – Aug) in 30 paired nest and random areas in northern Arizona. Owl nest areas were significantly cooler than random areas, and evaporative water loss modeled for Mexican spotted owls was significantly lower in nest than in random areas.

Potentially conflicting with this hypothesis is the presence of owls in canyons and riparian areas at relatively low elevations (e.g., Willey and Ward 2004, Bowden 2008). Although owls appear to select microsites in these canyons that are cooler than surrounding areas, summer daytime temperatures in some of these areas become quite warm. However, 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 (Weathers et al. 2001), 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. 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). Individual owls that select roosting and nesting sites that are also closer 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 these other factors (see also Carey et al. 1992, Zabel et al. 1995, Ganey et al. 1997, Ward et al. 1998, Ward 2001, May et al. 2004).

E. Habitat Models

A number of efforts have been made to develop and test predictive models for Mexican spotted owl habitat. These efforts have been conducted independently and were not coordinated until recently. Although specific objectives and approaches differ among efforts, most have focused on nesting and roosting habitat, because of the apparent importance of this type of habitat in explaining owl distribution (USDI FWS 1995). Efforts and models can be loosely grouped by six sets of investigators as discussed briefly below.

a. Terrell H. Johnson.—From 1988 to 2003, T. H. Johnson developed a series of predictive models for Mexican spotted owl habitat. This series of models began with a timber-type model for the Jemez Mountains, New Mexico (Johnson and Johnson 1988, refined and expanded in Johnson 1990). The timber type model predicted availability of suitable habitat within these mountains based on USDA FS stage 1 timber inventory data. Johnson and Johnson (1988) reported that the model successfully discriminated owl from random sites and concluded that it could prove useful in other areas with available timber inventory data.

The timber-type model was superseded by a topographic model of potential owl habitat throughout New Mexico, with model predictions based on topographic characteristics derived from a 1-degree digital elevation model (DEM; Johnson 1993). This model again showed promise for predicting potential owl habitat, and it had the decided advantages that it was based on topographic data available for all land ownerships and might explain owl distribution better in canyon landscapes than did vegetation data. Johnson (2001) tested this model across the range of the owl in the southwestern U.S., using a database of owl locations compiled in 1993 in conjunction with recovery planning efforts (Ward et al. 1995). The model generally performed well in New Mexico and eastern Arizona, but accuracy declined along an east to west gradient. Johnson (2001) concluded that a longitudinal function should be included in future models and that such models should be based on higher-resolution topographic data.

Johnson (1996) reformulated the topographic model for higher-resolution 7.5-minute DEM data in northern New Mexico, then added Landsat imagery to a model covering the Los Alamos National Laboratory, New Mexico (Johnson 1998). Later, he developed a geophysical model of potential owl habitat for the southwestern U.S. (Johnson 2003). This model used the higher-resolution (7.5-min) topographic data and used variables related to winter and summer
precipitation to model the east-west gradient observed in tests of the earlier topographic model throughout the southwest (see Johnson 2001). This model performed reasonably well in tests using independent owl locations. The model assigned a potential habitat index to locations, rather than simply defining habitat as suitable or unsuitable, which may allow greater flexibility in using the model. Johnson (2003) noted that coordinates of some of the locations used in model development likely were recorded inaccurately or imprecisely and that this error hampered the model’s ability to discriminate between owl and background sites. He suggested that future models could be improved simply by eliminating spatial error in owl locations and by incorporating additional data resulting from ongoing survey and research efforts on Mexican spotted owls.

b. David W. Willey and Colleagues.—D. W. Willey and colleagues also developed and tested a series of Geographical Information System (GIS)-based models based largely on topographic characteristics, with their efforts focused on the canyonlands of the CP. Their initial model identified predicted breeding habitat for owls throughout the state of Utah based on physical landscape features (Willey and Spotskey 1997). The model identified three habitat classes: predicted breeding habitat, predicted marginal habitat, and predicted non-habitat. The model incorporated data on slope, aspect, slope curvature (an index of ruggedness), and crude vegetation (e.g., forest, shrubland, or grassland). This model was designed to predict the general location of breeding habitat across large landscapes, and it was not intended for use at finer spatial scales (Willey 2002a).

Subsequent efforts expanded that modeling effort to cover northern Arizona as well and focused on producing a model that could be used at multiple spatial scales (Willey and Spotskey 2000, Willey 2002a). This model incorporated data on slope, aspect, slope curvature, vegetation at the species association level, surface geology, soil moisture, and an index of surface temperature (Willey 2002a). Tests of this model using different techniques and in different areas suggested that it was useful at identifying owl breeding habitat in canyon landscapes at relatively fine scales (<1:100,000; Willey and Spotskey 2000, Willey 2002b). However, Willey and Weber (2003) noted that predictions generated confusion among land managers, so they developed a third-generation model using finer-grained spatial data. Field tests of this model were conducted during 2004 with mixed results. In several cases, owls were not detected where probabilities of suitable roosting or nesting habitat were predicted to be high. This result could have been due to a year of low occupancy caused by factors independent of habitat suitability, however (e.g., Willey and Willey 2010). A more refined procedure was used in 2005 to generate and select among competing models developed with different geomorphological and vegetation-based variables. Models with the best performance based on two different selection criteria (Akaike’s information criterion [AIC] versus a stepwise optimization procedure) produced similar results. In either case, maps based on confidence intervals (e.g., 95% or 99%) for prediction of occupancy could be produced. Percent slope was found to be the most useful variable in predicting owl roosting and nesting habitat regardless of model selection technique. The steepest slopes were identified as the most likely locations to find Mexican spotted owls in the study canyons of Utah.

Willey et al. (2007) further refined this model, again using model selection to rank competing GIS-based habitat models. Model parameters were generated using geomorphological and
vegetation-based habitat variables, and habitat associations were identified by comparing occupied and unoccupied sites located during extensive field surveys (Willey et al. 2007). The set of habitat covariates included: 1) landscape ruggedness, slope, and complexity (Rinkevich 1991, Willey 1998b); 2) relative surface temperature and presence of cool zones (Rinkevich 1991, Willey 1998b); and, 3) vegetation cover, which provides shelter as well as microenvironments for prey species (Ganey and Balda 1989b, Willey 1998b, Ganey et. al 2004). Willey et al. (2007) used model averaging across the three top habitat models to produce a predictive equation to identify potential Mexican spotted owl habitat in canyon terrain within the Utah study areas. The probability of owl occupancy was strongly and positively associated with percent slope and negatively associated with elevation range and selected vegetation covariates. Field testing included surveys in 487 1-km² (247 ac) test plots with 1,430 calling stations distributed across 22 U.S. Geological Survey quadrangle maps during the 2007 field season. Mexican spotted owls were detected in 14 quadrangles, including 57 owl detections within 22 individual test plots. The mean habitat suitability for the 22 test plots as estimated by the best approximating model was 60% (SD = 25%). In addition, 70% of the owl detections occurred within plots whose average suitability score was >50% and, for the 22 occupied study plots, only six showed habitat suitability less than 50%.

c. Tim Mullet.— In more recent work, Mullet (2008) examined the applicability of the two models described above (Johnson 2003, Willey et al. 2007) for predicting occupancy of Mexican spotted owls in the Guadalupe Mountains of southeastern New Mexico and West Texas. This work focused primarily on the zones of high-probability (>75%) of owl occurrence predicted by the two models. The two models produced slightly different maps of predicted habitat, with some (overlapping) areas predicted to contain suitable habitat by both models. Mullet (2008) used formal occupancy surveys (during a single breeding season, in a random set of 25, 2-km² (494 ac) survey cells, each with two to five stations) and modeled detection probabilities and the probability of site occupancy for each survey cell using various covariates. Covariates included the amounts of high-probability predicted habitat from a given model in each cell. Despite being smaller than the area predicted separately by either model, the overlapping area of habitat predicted by both models provided the same level of accuracy and precision as either model separately. This area of overlap between the two models primarily coincided with narrow, steep-walled canyons. Mullet (2008) therefore concluded that both models were useful for identifying habitat that had a high-probability of being occupied, but that the area of overlap of the two predicted habitat maps was much more efficient than either model alone in predicting habitat that would be occupied by Mexican spotted owls in the Guadalupe Mountains.

d. Joseph L. Ganey and Colleagues.—Efforts by this group focused on National Forest System (NFS) lands in northern Arizona. In an early effort, Ganey et al. (1990, see also Ganey 1991) used GIS, a DEM, and Landsat multispectral scanner imagery to develop a predictive model for Mexican spotted owl habitat on four National Forests in north-central Arizona. Model output was a spatially explicit map of predicted owl habitat. The model defined suitable owl habitat as occurring where slope was >15% and cover type was dense mixed-conifer, ponderosa pine, or deciduous forest. Ganey (1991) tested this model at the landscape scale by evaluating agreement between model predictions and independent survey locations of Mexican spotted owls (i.e., locations not used in
model development). Prediction accuracy generally was high in mixed-conifer forests, intermediate in pine-oak forests, and lowest in rocky-canyon areas.

Ganey (1991) also tested the model using data from eight radio-marked owls representing five territories in three study areas. Owl locations occurred in predicted habitat significantly more than expected by chance at four of these sites. Agreement between model predictions and owl locations was low at the fifth site, where the owls occupied a rocky canyon. He concluded that the model could be used to prioritize general survey areas, and might be useful for identifying specific areas for habitat protection in mixed-conifer forest, but it was not useful at that scale in rocky-canyon landscapes. This relatively crude model was used by forest biologists to prioritize survey areas but was not developed further.

Ganey and Benoit (2002) evaluated the use of Terrestrial Ecosystem Survey (TES) data to identify potential Mexican spotted owl habitat on NFS 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 survey database [USDI FWS 1995], locations of radio-marked owls, and results from complete surveys of selected quadrats [Ganey et al. 2004]), they identified subsets of map units that were strongly associated with owl use on three national forests in northern Arizona. These map units generally consisted of mixed-conifer or pine-oak forest, and those most strongly associated with owl use generally occurred on steep slopes containing rocky outcrops. Ganey and Benoit (2002) concluded that, with some caveats, TES data could be used to identify and map potential owl habitat.

e. William J. Krausmann and Colleagues.—William J. Krausmann and colleagues also focused on NFS lands, but their modeling efforts were specifically directed at assessing gross changes in amounts of Mexican spotted owl habitat over time (i.e., change detection, Krausmann et al. undated, Mellin et al. 2000). Thus, their efforts focused on products that could be used to monitor changes in amounts of owl habitat over time. They identified forest types “associated” with Mexican spotted owls on NFS lands in Arizona and New Mexico, using TES (see above) and Generalized Ecosystem Survey data (essentially a coarser-scale version of TES) and USDA FS 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 et al. 2000).

Approximately 28.2% of NFS lands within Arizona and New Mexico were identified as belonging to vegetation units associated with Mexican spotted owls. Within those vegetation units, 4.2% underwent some form of vegetation removal or reduction over the five-year period, for an annual rate of change of <1%. 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.

The conclusions regarding changes in amount of owl habitat depend heavily on the assumptions about which vegetation units were associated with Mexican spotted owls. The accuracy of these assumptions, and the resulting classification of “owl-associated” habitat, is unknown. To address this uncertainty, Mellin et al. (2000) also summarized change based on the area
contained within owl PACs. This analysis, which included nine national forests that had digitized GIS coverages of PAC boundaries, avoids the need to classify habitats as associated or not associated with owls. Vegetation removal or reduction occurred on 3% of the total PAC area, with 80, 14, and 5% of the change due to fire, mechanical treatments (timber harvest and/or thinning), and infestations of forest insects or pathogens, respectively.

The modeling effort by Krausmann and his colleagues demonstrated that Landsat imagery could be used to detect gross changes in owl 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, no follow-up efforts have occurred, nor are there any plans to conduct follow-up analyses (W. J. Krausmann, pers. comm.). Further, 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 would obviously be important in a comprehensive effort to monitor trend (including both gains and losses) in owl habitat.

f. **Forest Ecosystem Restoration Analysis Project (ForestERA).**—The Forest ERA program also developed a predictive model for Mexican spotted owl habitat covering a study area of approximately 8,100 km² (2 million ac) near Flagstaff, Arizona. ForestERA is a collaborative project headquartered within the Center for Environmental Science and Education at Northern Arizona University. It provides data, tools, and analytical frameworks for developing landscape-level strategies for ecosystem restoration, and assessing the impacts and implications of alternative management scenarios (Sisk et al. 2004). This program modeled Mexican spotted owl habitat as one data layer facilitating landscape-level assessments within their Western Mogollon Rim study area (Prather et al. 2005). The model defined Mexican spotted owl nesting and roosting habitat as areas where the dominant overstory vegetation consisted of pine-oak, mixed-conifer, or ponderosa pine cover types on steep slopes (>12 degrees), and where basal area exceeded 17 m² ha⁻¹ (75 ft² acre⁻¹). Predicted habitat was assessed using the Mahalanobis distance statistic and vegetation (tree density, canopy cover, basal area) and terrain (slope, aspect) characteristics around known owl nest sites. This statistic was used to determine how divergent a given location on the landscape was compared to the typical characteristics of the landscape at known nest sites, and it allowed them to assess the likelihood that owls would use a particular area. Preliminary assessments of model accuracy suggested that it successfully predicted the locations of most owl nest and roost sites, despite classifying only about 30% of the assessment area as nest/roost habitat (Forest ERA 2005).

ForestERA also produced a spatial coverage representing management definitions of Mexican spotted owl habitat across the assessment area. This data layer depicted habitat categories as defined in USDI FWS (1995). Categories modeled included protected habitat, restricted habitat, and areas with no specific owl-related guidelines (other forest and woodland types; USDI FWS 1995). This allowed for comparisons of overlap between predicted habitat and areas managed for owls under USDI FWS (1995). Although no quantitative analysis is available, a visual comparison of maps of predicted habitat and management guidelines suggests that 1) areas managed for Mexican spotted owls under USDI FWS (1995) cover less of the assessment area than is predicted to contain nesting and roosting habitat for owls, and 2) areas managed as protected or restricted habitat for owls generally are predicted to be owl habitat (Fig. B.5).
ForestERA recently updated this coverage based on definitions in this revised Recovery Plan. Results again indicated that plan recommendations target a relatively small proportion of the study area (approximately 20%; see Appendix C).

g. Other Recent Efforts.—Two other recent efforts focused on developing habitat models at more localized scales. Danzer (2005) used existing data on owl occupancy, fire history, and site characteristics to describe features of Mexican spotted owl territories in the Huachuca Mountains, Arizona. Owl territories were variable, but most occurred in canyons with riparian, mixed-conifer, and oak components, a finding consistent with previous analyses in this region (Ganey and Balda 1989a: Fig. 2, Duncan and Taiz 1992, Ganey et al. 1992, Ganey and Dick 1995: Table 4.1). Hathcock and Haarmann (2008) developed a vegetation-based predictive model for Mexican spotted owl habitat in the Jemez Mountains, New Mexico. Compared to random sites, sites used by owls had greater tree species diversity, tree density, tree height, canopy cover, and shrub density. Again, these features generally agree with other evaluations of owl habitat, both locally and in a broader sense. Model testing suggested that the model performed adequately, and Hathcock and Haarmann (2008) suggested that this model could be used to delineate habitat on a relatively fine scale.

h. Summary of Mexican Spotted Owl Habitat Models.—In summary, a number of predictive models have been developed for Mexican spotted owl habitat. Modeling efforts have occurred throughout much of the range and have incorporated many different approaches and objectives (e.g., prediction of breeding habitat versus change detection). These efforts have produced a number of useful products, including maps of predicted habitat for different areas and maps useful in detecting changes in habitat amount or condition. The ongoing efforts by T. H. Johnson and by D. W. Willey and colleagues appear to hold considerable promise for future efforts. Both also 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. Models incorporating topography have the advantage that they are based largely on topographic and/or climatic data that are available for all land ownerships across the range of the owl. The recent work by Mullet (2008) demonstrated the utility of these types of models in predicting occupancy of Mexican spotted owls in the Guadalupe Mountains and how structured validation surveys can lead to a more efficient model. In this case, the overlap between habitat predicted by two models provided the most efficient model (i.e., a model with less predicted habitat to search while conveying the same probabilities of occupancy).

In some areas, data on vegetation type and composition may improve models significantly. For example, the model produced by Forest ERA used data on vegetation structure and composition to model nesting and roosting habitat structure. These types of data are not as readily available as topographic data and typically require analysis of satellite imagery to derive useful data layers (Forest ERA 2004). Such data also can be used to detect changes in vegetation structure, however, and this ability would be critical in efforts to monitor amounts and distribution of Mexican spotted owl habitat. That is, topographic models can be used to model potential owl habitat, but they cannot effectively model current owl habitat except in areas where topography is more important than vegetation, such as in the canyonlands.
Figure B.5. Maps of predicted Mexican spotted owl nesting and roosting habitat (top) and management guidelines (bottom) for Mexican spotted owls under USDI FWS (1995). Source: Forest ERA 2005.
The habitat models developed also have produced some useful insights unrelated to their original intent. For example, Ganey and Benoit (2002) noted that TES data identified most of the map units strongly associated with owl use in their study area as not well suited for timber harvest, due to either steep slopes or soil-based considerations. Similarly, comparison of owl-related maps with other maps produced by Forest ERA suggests that there is high overlap between owl habitat, either as predicted by their habitat model or as defined based on protective categories in USDI FWS (1995), and predicted habitat for the northern goshawk (Fig. B.6, top), a species of special management concern (e.g., Reynolds et al. 1992). Another such comparison suggests that species diversity of breeding birds is generally greater in owl habitat than elsewhere (Fig. B.6, bottom). Together, these results suggest that 1) it might be feasible to protect owl habitat while simultaneously minimizing impacts to timber harvest programs, and 2) this protected habitat appears to be particularly important to other wildlife species of interest as well. Finally, the owl habitat coverages developed by ForestERA also allowed Prather et al. (2008) to evaluate potential conflicts between management to reduce fuels and risk of severe wildland fire and management to retain Mexican spotted owl habitat. This analysis demonstrated that although some conflicts exist between these objectives, their magnitude has been overstated (see also Appendix C). They concluded that the majority of the landscape could be managed to reduce fire hazard without eliminating owl habitat (see also James [2005] for a concurring view).

F. 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 (Krausmann et al. undated, Mellin et al. 2000) suggested that wildland fire, mechanical treatments, and forest insects and pathogens (in that order) were key disturbance agents affecting owl habitat. Other potential disturbance agents that may threaten the owl indirectly through habitat alteration include heavy grazing by domestic livestock and 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. If habitat alteration is extensive, habitat loss can result in negative impacts on Mexican spotted owl populations by limiting the number of occupants and their reproduction. Indeed, presumed habitat loss due to timber harvest was one of the factors that precipitated listing the owl as threatened (USDI FWS 1993).

The majority of disturbance agents that can alter Mexican spotted owl habitat are discussed elsewhere in this Recovery Plan (Parts I and II). No studies are available on the specific effects of forest insects and pathogens on this owl’s habitat, few studies have evaluated effects of mechanical treatments on spotted owls, and none of these studies focused specifically on Mexican spotted owls. As a result we know relatively little about the effects of these disturbance agents on the owl and its habitat. However, several studies or analyses have focused on wildland fire, which appears to have the greatest potential to greatly alter the owl’s habitat over vast areas in a relatively short time period (e.g., Krausmann et al. undated, Mellin et al. 2000). Therefore, this disturbance agent and its potential influence on the ecology of Mexican spotted owls warrants specific discussion. There also is limited information about four other disturbances that may influence the owl’s habitat: mechanical treatments, heavy grazing by domestic livestock and
wild ungulates, urban development, and shifts in biological communities caused by climate change. Below, we discuss the potential influences of these four disturbance agents.

a. Wildland fire and Prescribed Fire.— Fire is a natural disturbance agent in southwestern forests (Swetnam 1990), with which Mexican spotted owls co-evolved. Ponderosa pine and xeric-mixed conifer forests evolved with a fire regime characterized by frequent-surface fires. Early Euro-American-settlement, overgrazing, and other land-use practices that began around 1880, followed by organized fire suppression and logging, have resulted in severely altered surface fire regimes and forest structure in these southwestern forest types (Rummel 1951, Madany and West 1983, Savage and Swetnam 1990, Covington and Moore 1994, Fulé et al. 2004). As a result, these forests have not experienced landscape-scale fire effects for over a century in many places and are now characterized by closed canopies with dense stands of small trees, and heavy forest litter and duff fuel loads. These widespread changes have resulted in substantially altered fire behavior and effects in these forests ecosystems. These forests are now very prone to stand-replacement, high-intensity and high-severity fires that are now very difficult to control. As a result, we have seen an increasing trend in the size and severity of wildland fires in the western U.S., including the Southwest (Westerling et al. 2006, Littell et al. 2009, Miller et al. 2009). This trend in the Southwest began around 1990 with the stand-replacing Dude fire in Arizona (> 2,400 acres), escalating in 2011 to the most intense and largest fires in Southwest history, as over 809,716 ha (2 million acres) burned in Arizona and New Mexico (USDA FS unpubl. data).

The real quandary is that fire is a double edged sword, potentially the savior and threat to the Mexican spotted owl. In essence low- to moderate-severity and even high severity fire patches on the fine scale (e.g., 1 to 100 acres) are likely desirable for more resilient forest landscapes and owl habitat. However, high severity patches over large areas (e.g., > 100 to 500 acres) may have cumulative effects on forest structure given recent trends that possible may not be beneficial to Mexican spotted owl recovery or sustainable forest management.

Recognizing these changing aspects of southwestern forest ecology and the potential for more and larger high-severity fires to occur in the near future, the Recovery Team recognizes stand-replacing wildland fire as one of the primary threats to the Mexican spotted owl and its habitat. The underlying assumptions are: 1) under some conditions stand-replacing wildland fire can severely alter forest stand structure and the attributes that Mexican spotted owls need for roosting and nesting; 2) replacement habitat could take centuries to regenerate given the age of forests and trees on these sites; and, 3) cumulative loss of large amounts of roosting and nesting habitat to wildland fire ultimately can be detrimental to spotted owls, even if they are able to persist in burned areas over the short term.

To better understand how much of the owl’s habitat could be affected by stand-replacing fire in the future, the Recovery Team quantified recent trends in burn-severity over a 14-year period (1995 to 2008) within 90% of established PACs (Box B.2; we were not able to obtain spatial data for the other 10% of known PACs). The analysis showed variability among the five U.S. EMUs, but the overall analysis indicates that >40% of current PAC area could be altered by high-severity fire in the BRW, SRM, and UGM EMUs, whereas less than 15% of habitat within PACs may be altered in the BRE and CP EMUs by 2110 (Box B.2, Fig. 1c). Projections that mega-fire
years like that observed in Arizona and New Mexico in 2011 will become increasingly more frequent could result in an exponential increase in rate of high-severity fire effects in PACs such that habitat within all currently designated PACs in the SRM and BRW EMUs could be burned by high-intensity fire within 40 to 90 years (Box B.2, Fig. 1d and e). In summary, high-severity fire effects will continue to impact PACs at an unknown, but likely, accelerated rate. Fuels reduction projects and previously burned areas distributed across the landscape may, over time, reduce the exponential trend of high-severity wildland fire effects in PACs. To slow or alter this increasing rate of high-severity fire effects, the potential for stand replacing fire needs to be significantly reduced on the landscape within 30 to 40 years. We reiterate, however, that the future trends of high-severity fire effects to Mexican spotted owls are largely unknown.
In this Recovery Plan, we presume that loss of habitat resulting from the effects of high-severity wildland fire is a threat to the Mexican spotted owl. High-severity fire effects include a high percent loss of site organic matter, canopy, and vegetation cover (i.e., stand replacement fire), and high tree mortality and exposure of soils (DeBano et al. 1998; Keeley 2009). Furthermore, the scale of high severity fire we have seen in recent decades in the ponderosa and more xeric mixed conifer forest ecosystems appears to be outside the historical range of variation (Fulé et al. 2004).

Understanding the magnitude of this threat requires knowledge of the following; 1) the rate and extent of high-severity fire affecting the owl’s habitat; 2) the effects of high severity fire on owl habitats, forest ecology and succession; and, 3) how the owl and its populations respond to these habitat alterations caused by high-severity fire effects. To better understand the potential magnitude of high-severity fire effects on the owl’s habitat, the Recovery Team examined recent trends in fire-severity within designated PACs. We quantified the number of PACs and amount of PAC area that were burned resulting in different severities of fire over a 14-year period (1995 to 2008) and then used the annual (estimated as a 14-year mean) rate of high-severity fire to project potential future losses of the owl’s habitat in 10-year intervals through 2110. The results of this analysis are presented below. We currently have no long-term data from which to assess how the forest habitat or the owls will respond to these stand-replacing high-severity fire events (see Appendix B for further discussion regarding this topic).

To estimate the amount of owl habitat burned from 1995 to 2008, we used the geospatial boundaries of PACs to identify the most important, and limiting, habitat to Mexican spotted owls, and we used annual boundaries of fires ≥ 405 ha (1,000 ac) to estimate area burned and fire severity effects. Wildland fire boundaries were derived from the standardized USGS Monitoring Trends in Burn Severity database (MTBS; http://mtbs.gov/index.html), which only tracks fires ≥405 ha. From the overlap of these two data sets, we estimated the amount and percentage of area burned annually in PACs over the 14-year period. We examined PACs from 17 different public land management units, including 12 National Forests (six in Arizona, five in New Mexico, one in Utah), BLM lands in Utah, and four National Parks (one in Arizona, three in Utah). The time period was chosen because it followed the release (and hence recommendations) of the original Recovery Plan (USDI FWS 1995) and because burn-severity data were not available beyond 2008. Unfortunately comparable fire severity data from the record-breaking 2011 fire season were not available, nevertheless preliminary evaluations of the 2011 fire severities further support these findings.

The MTBS data included five general classes of burn-severity effects on vegetation: 1) unburned or undetected, 2) low, 3) moderate, 4) high, and, 5) burned, but with unknown severity (Eidenshink et al. 2007). To project future loss of owl habitat, we used the rates of high-severity fire effects estimated annually from the 14-year period to estimate the percent of PAC area that would be burned in future 10-year increments, assuming four scenarios. The first scenario assumed that the area burned by fire was fixed during each 10-year period and equal to the amount of area burned in each EMU during the initial 14-year period. In the second scenario, we assumed an exponential increase of 1% of additional PAC area burned each year than under the constant rate scenario. The third scenario assumed an exponential increase of 4 percent of additional PAC area burned each year. The final scenario assumed that the amount of PAC area impacted by high-severity fire effects would increase exponentially (4% annual increase), but would slow and eventually plateau after 40 years of increasing wildfire trends, fuels reduction and restoration treatments. We focused on high-severity fire effects because they result in the most significant alteration of owl habitat and hence, have the greatest potential for loss of habitat.
Our analysis included 1,174 PACs 89% of the 1,324 known owl sites) and encompassed 329,054 ha (812,763 ac) (Table 1). During the 14-year period of 1995 to 2008, a total of 50,034 ha (123,632 ac) burned in 438 of the PACs. The percentage of habitat area burned by any type of fire was lowest in the CP EMU, where owl nest/roost habitat occurs more frequently in rocky canyons, which are less likely to burn than forested habitats (Figure 1a).

On average, low-severity fire effects were detected over the largest percentage of hectares and high-severity fire were detected in the lowest percentage of hectares within the burned PAC areas (Table 1). Large-fire years were observed in 2000, 2002, and 2004 and on average more PAC area burned with high-severity fire effects in these years (Figure 1b). The annual percentage of PAC area affected by high-severity fire varied among EMUs during the 14-year period (Table 2). The greatest percentage of PAC area affected by fire was in the BRW EMU (Figure 1a).

Projections about future extent of high-severity fire effects (constant rate of increase) under the first assumption indicated that modification of the owl’s habitat during the next century in the five U.S. EMUs could range from 2 to 56 percent of current PAC area (Figure 1c). Projected losses, assuming the 1 percent-exponentially increasing rate of high-severity fire effects indicated that by 2110 all PACs in the SRM and BRW could be burned, that nearly 80% of the PAC area in the UGM could be burned, and that <30% of the PAC area could be burned in the CP and BRE EMUs (Figure 1d). Under the more extreme scenario of a 4 percent annual exponential increase, 100 percent of PAC area would be affected by high-severity fire in the SRM and BRW EMUs by 2065 and in the UGM EMU by 2075 (Figure 1e). Under this scenario much of the remaining PAC area not affected by high-severity fire would be in the CP EMU. The extreme scenario of 4% exponential increase could slow and begin to stabilize following the 40 years of increase if fuels reduction treatments are effective and/or high-severity fire effects are limited by the previous wildfire effects at an exponentially decreasing annual rate of about 2 percent (Figure 1f).

Although these projections are based on very simplistic assumptions and forecasts, the analysis is useful for showing: 1) past conditions and fire behavior varied by EMU, likely because of differences in fuel sheds and burning conditions related to elevation, weather, topography, and vegetation; and, 2) to date, high-severity fire effects in PACs have been relatively rare rangewide. Unfortunately, our analysis was not able to include fire data from 2011 because comparable data are not yet available. Although the extent of high-severity fire effects in PACs is not known for the 2011 fires, the number of PACs that experienced large (> ⅔ of PAC area) fires easily could double beyond the number recorded for our analysis period. Our results also indicated that under the conditions present from 1995 to 2008, owls dwelling in canyon habitats were least impacted by high-severity fire effects (i.e., the CP EMU), and the EMU’s where the majority of owls are concentrated (e.g., UGM and BRE EMUs), experienced lower rates of high-severity fire than the BRW or SRM EMUs. However, the projected rates of habitat alteration for the future are rough estimates and the amount of habitat affected by high severity burns was not offset by restored or newly developed habitat over this analysis period. These data suggest that under climate-warming forecasts and less-conservative rates of high-severity fire effects, Mexican spotted owl habitat degradation could escalate in most portions of the range in the foreseeable future. Alternatively this undesirable habitat loss could potentially be mitigated if future wildfire effects are moderated under wetter decadal-climate regimes and more effective at reducing forest fuels and opening forest canopies rather than replacing them, and if strategically placed treatments across the landscape are more influential in slowing and reducing the size of future high-severity fire patches.
### Box B.2, Table 1. Cumulative fire severities (ha) in Mexican spotted owl habitat (PAC area), 1995-2008.

| EMU | No. PACs | PAC Area (ha) | Burn Severities within PAC Area (ha) | | | |
|-----|----------|---------------|--------------------------------------|---|---|---|---|
|     |          |               | Low | Moderate | High | Any |
| CP  | 132      | 52,642        | 562 | 327      | 109  | 998 |
| SRM | 50       | 13,668        | 909 | 726      | 999  | 2,634 |
| UGM | 684      | 181,730       | 14,743 | 8,535 | 8,264 | 31,540 |
| BRW | 155      | 43,193        | 5,746 | 5,129 | 2,653 | 13,527 |
| BRE | 153      | 37,821        | 344 | 340      | 650  | 1,335 |
|     | Totals:  | 1,174         | 329,054 | 22,304 | 15,057 | 12,675 | 50,034 |

14-yr % of PAC Area:
1. Calculated by dividing the total area burned over 14 years under each severity by the total amount of PAC area in an EMU.
2. Calculated by dividing the 14-yr percentage of PAC area burned by 14.

### Box B.2, Table 2. Percent of Mexican spotted owl PACs that burned with high severity fire effects, 1995-2008.

<table>
<thead>
<tr>
<th>EMU</th>
<th>No. PACs</th>
<th>% of PACs with high-severity fire effects</th>
<th>% PAC area with high-severity fire effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>None</td>
<td>1–79 ha</td>
</tr>
<tr>
<td>CP</td>
<td>132</td>
<td>92.4</td>
<td>7.6</td>
</tr>
<tr>
<td>SRM</td>
<td>50</td>
<td>78.0</td>
<td>10.0</td>
</tr>
<tr>
<td>UGM</td>
<td>684</td>
<td>72.0</td>
<td>22.4</td>
</tr>
<tr>
<td>BRW</td>
<td>155</td>
<td>50.3</td>
<td>41.3</td>
</tr>
<tr>
<td>BRE</td>
<td>153</td>
<td>91.2</td>
<td>5.2</td>
</tr>
</tbody>
</table>

Total PACs: 1,174
873 | 240 | 49 | 12
Box B.2, Figure 1: (a) Mean percentage (± SE) of Mexican spotted owl PAC habitat burned in each of 5 EMUs from 1995 to 2008 and (b); annual trend in high-severity fire effects and fire in PACs from 1995 to 2008. Projected percent of PAC area burned resulting in high-severity fire effects through 100 years assuming: (c) a constant rate of increase equal to the EMU annual rate; (d) an exponential increase of 1% per year above the EMU annual rate; (e) an exponential increase of 4% annual increase per year above the EMU annual rate; and, (f) initial 4% exponential increase followed by asymptotic decrease under the assumption of forest treatment or disturbance effects after 40 years exponentially increased rates of high-severity burn effects. CP = Colorado Plateau, SRM = Southern Rocky Mountain, UGM = Upper Gila Mountain, BRW = Basin and Range-West, BRE = Basin and Range-East.
Understanding the impact of wildland fire on Mexican spotted owls also requires knowledge of the owl’s response to fire. Since 1995, several studies have examined short-term effects of fire on Mexican spotted owls. Here, we summarize briefly the important results of those studies and re-evaluate the importance of fire as a threat to owl habitat based on these results. Additional recent studies have evaluated or speculated on fire effects and/or historical disturbance patterns affecting northern and California spotted owls (Elliott 1985, Buchanan et al. 1995, MacCracken et al. 1996, Bevis et al. 1997, Everett et al. 1997, Gaines et al. 1997, Verner 1997, Franklin and Gutiérrez 2002, Irwin and Thomas 2002, Irwin et al. 2004, Lee and Irwin 2005, Clark 2007, Bond et al. 2009). We restricted our evaluation here mainly to studies on the Mexican spotted owl, because of regional variation in fire regimes and the resulting apparent differences in this owl’s environment compared to that of the other two subspecies. However, we include results from two recent studies on other subspecies of spotted owls (Clark 2007, Bond et al. 2009) because these studies evaluated fire effects more rigorously than previous studies, and their results have potentially important implications.

To date there have been at least seven studies or other evaluations on the effects of fire on Mexican spotted owls. These studies occurred in four EMUs, in a variety of geographic locations and forest types, and have included both wildland fire and prescribed fire. Studies are discussed below in chronological order.

Johnson (1995:5–6) did not study fire effects explicitly but discussed fire and Mexican spotted owls in the area impacted by the 1977 La Mesa Fire in the Jemez Mountains, New Mexico (SRM EMU). Two territories within the boundary of this fire were occupied more consistently than other territories in the Jemez Mountains in the decade from 1985–1995. Data on owl reproduction were not sufficient to compare reproduction at these territories to other territories within the region, and owls were not marked, so survival data were not available from these territories. Owls were sometimes observed roosting in burned areas and were heard at night in burned areas on the mesa. Thus, at least some territories were occupied following the fire, and owls appeared to forage and occasionally roost in burned areas.

Sheppard and Farnsworth (1997) discussed potential impacts of fire on owls. They estimated that at least 10 Mexican spotted owl territories were impacted by fire in Arizona and New Mexico during the 1994 fire season. They further estimated that >20,000 ha (>50,000 ac) of owl habitat experienced stand-replacing wildland fire from 1989 to 1994. They did not evaluate patterns of owl habitat use or territory occupancy relative to these fires, however.

Willey (1998a) tracked three pairs of radio-marked Mexican spotted owls before and after prescribed burns in Saguaro National Park, southern Arizona (BRW EMU). These burns increased canopy edge and structural diversity within stands (Willey 1998a:30–31). They created openings within the forest, but these openings were very small (<1 ha [2 ac]) relative to the size of owl home ranges (125 to 545 ha [310 to 1350 ac] pre-fire; Willey 1998b: Table 6), and no burning was done in the north-slope mixed-conifer forests where owls roosted and nested. Home range and activity centers decreased in size for two of three pairs following the burns, but increased for the third pair. Home range centroids shifted from 100 to 500 m (300 to 1500 ft) for all pairs. However, Willey (1998b) noted that both range shifts and changes in range size could be confounded by changes in nesting status pre- and post-fire, and he generally regarded these
results as inconclusive. Clearly, however, owls continued to use these areas following relatively low-intensity prescribed burns that occurred outside of nest/roost areas, at least in the short term.

Bond et al. (2002) documented minimum survival and site and mate fidelity for four pairs of color-marked Mexican spotted owls in Arizona and New Mexico (UGM EMU) after large wildland fires (>525 ha [1,300 ac]). 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 fourth 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%. Results were similar for northern and California spotted owls that experienced wildland fire on their territories (Bond et al. 2002). Thus, owls studied continued to occupy burned areas, even following relatively high-severity fires, except in the territory that experienced the highest burn severity. Results further suggested that survival rates and mate and site fidelity in these owls were relatively high in the year following fire.

Jenness et al. (2004; see also Jenness 2000) surveyed historical Mexican spotted owl territories (as delineated by USDA FS 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 UGM, BRW, and BRE EMUs. 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 (21 vs. 16%) and almost twice as likely to be unoccupied as were unburned territories (30 vs. 16%). These differences were not statistically significant, but the significance test had low power due to small samples of sites (Jenness et al. 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, three sites where >50% of the territory burned contained reproducing pairs, and a single owl was present at the most severely burned territory. No variables related to fire severity appeared correlated with patterns of occupancy or reproduction. These results again 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 USDA FS, however, 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.
Ward and Moors (2011) reported on occupancy and reproduction of Mexican spotted owls dwelling in burned and unburned landscapes in the Pinaleño Mountains of southeastern Arizona, based on a single season of survey in 2011. Their study area included the Nuttall-Gibson fire that occurred in 2004, 7 years prior to their survey. Seventeen PACs were included in their analysis and these ranged from 99% of the included area burned to 100% unburned, and high-severity burn ranged from 2.5 to 38.5% of area within the PACs. Pairs occurring in PACs with more burned habitat averaged 1.75 young/pair and included the only pair that had 3 young that year. Pairs in PACs with <4% of the habitat burned had an average of 1.33 young/pair. Owl density appeared greater in the portion of the landscape that burned, and anecdotal information indicated that numbers of *Peromyscus* spp. were high in 2011. Thus, owls continued to occupy and reproduce in burned areas. The authors noted that any potential benefits of burned habitat was of unknown duration, and encouraged monitoring of post-fire development of ground vegetation and small mammal communities in burned areas, to better understand the potential effects of fire in owl habitat.

Recently, Clark (2007; see also Clark et al. 2011) studied territory occupancy, survival, reproduction, and habitat use by northern spotted owls in both burned and unburned landscapes in southwestern Oregon. The study area included a mosaic of public and private lands, some of which had an extensive history of past timber harvest resulting in a high degree of fragmentation of older forest habitat. In addition, many burned areas in this landscape were subjected to clearcut salvage logging.

Territory occupancy rates declined rapidly following wildland fire. Annual survival rates were substantially lower for owls within the burn (0.69 ± 0.12) or displaced by the burn (0.66 ± 0.14), relative to owls that lived adjacent to the burn (0.85 ± 0.06; Clark et al. 2011). No differences were observed between productivity of owls in burned and unburned landscapes. Clark (2007) noted that he was unable to estimate the impacts of wildland fire and salvage logging separately on northern spotted owl survival or territory occupancy, “…because they were highly interrelated and I lacked sufficient data to model these effects separately.”

Radio-marked owls used burned areas, but generally selected for either unburned forests or forests that burned with low severity and had little or no overstory canopy loss (Clark 2007:112). Radio-marked owls used areas that had been salvage logged less than expected based on their availability (Clark 2007:127). Clark et al. (2011:44) suggested that “…the combination of past timber harvest, severe fire, and salvage logging were responsible for the low survival rates during our study…”. They noted that the landscape studied had a high degree of habitat fragmentation prior to the fires and salvage logging (Clark et al. 2011:45), and stated that “…we urge caution when applying our findings to forest management or recovery planning for spotted owls.”

Bond et al. (2009) monitored movements and habitat use of radio-marked California spotted owls from four territories in the southern Sierra Nevada, California, four years following a large wildland fire. Study areas were not subjected to salvage logging (personal communication from J. P. Ward, Jr., 9 Sep 2011). Owls nested in all four territories, but only one pair was successful, fledging a single young. Two nests were located in moderate-severity burned mixed-conifer forest: one in low-severity burned mixed-conifer forest and one in unburned mixed-conifer-
hardwood forest. Owls roosted selectively in low-severity burned forest, avoided moderate-severity and high-severity burned forest, and used unburned forest in proportion to availability. Within 1 km (0.6 mi) of their nest, owls foraged selectively in all severities of burned forests and avoided unburned forests. These results collectively suggest that post-fire landscapes contained enough suitable habitat to support pair occupancy and at least attempted nesting. They further suggest that burned areas may provide benefits to foraging owls. Bond et al. (2009) concluded that assessments of fire impacts should not assume that all fires have negative impacts on spotted owls and recommended that burned forests within 1.5 km (0.9 mi) of spotted owl roosts or nests not be salvage-logged.

USDA FS (2010) reported on short-term results of surveys for California spotted owls (referred to in USDA FS [2010] as “CSOs”) in two areas burned by wildland fires in 2007 in the Sierra Nevada. One area (MACFA) was largely burned by high-severity wildland fire, whereas the second area (COFCA) burned primarily at low-moderate severity. Surveys in 2008 and 2009 located only a single pair of owls in the 35,612-ha (88,000-ac) MACFA fire complex. Single males were detected at night within the fire perimeter on several occasions in 2008, but not in 2009. None of these males were ever located at nests or roosts in follow up surveys, and none of the nocturnal locations occurred within 0.8 km (0.5 mi) of each other. In contrast, surveys of a 1.6-km (1.0 mi) buffer area around the fire complex located 5 confirmed pairs in 2008 and 7 confirmed pairs in 2009, along with additional sites where pairs could not be confirmed but there was evidence of territorial birds. Thus, owls were present in the general area, but showed little use of the severely-burned area.

In the first year of surveys (2009) in the 8,500-ha (21,000-ac) COCFA fire complex, six territorial owl sites were documented within the fire perimeter (3 confirmed pairs, one unconfirmed pair, and two single males), along with three confirmed pairs and three single territorial owls in the buffer area around the fire. In 2010, survey extent in this area was limited by safety concerns related to illegal marijuana cultivation. Nevertheless, surveys still located two confirmed pairs and one unconfirmed pair within the fire perimeter, and two confirmed pairs and one unconfirmed pair within the buffer area. Thus, owls in this fire area occurred in much greater density than owls in the MACFA complex. They also occurred in roughly similar amounts in the fire area and the buffer, in contrast to the MACFA complex, where most owls occurred in the buffer area. USDA FS (2010) concluded that “…CSO are able to persist in landscapes that experience primarily low/moderate severity wildland fire, whereas landscapes that experience primarily high-severity do not support comparable numbers or distribution of CSOs.”

In addition to the above studies, there are numerous anecdotal observations of Mexican spotted owls occupying territories following wildland fires and prescribed burns (P. Boucher, Gila National Forest retired, pers. comm.; S. Hedwall, FWS, pers. comm.), as well as evidence of radio-marked owls moving into and foraging in burned areas during winter (J. P. Ward, Jr. and J. L. Ganey, RMRS, unpubl. 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. However, 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. The sparse data
available from other subspecies are not entirely consistent, and are complicated by differences among study areas in both pre-and post-fire management (i.e., whether or not areas were salvage logged; see Clark 2007, Bond et al. 2009). Further, the effect of fire likely varies greatly with fire severity and spatial pattern. That is, fires that burn large areas with high severity likely have a greater impact than fires that burn primarily at low to moderate severity (USDA FS 2010), 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 the latter case, Bond et al. (2009) suggest that effects on owls may be largely positive by increasing prey access in areas proximal to nests or roosts (see Prey Habitat below). Finally, spotted owls in general show high site fidelity (Gutiérrez et al. 1995). Because of this, owls might continue to occupy burned territories even if the habitat 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.

b. Thinning/Timber Harvest.—Empirical data on the effects of thinning and other mechanical forest treatments on Mexican spotted owls are nonexistent. This is unfortunate, because thinning and other mechanical forest treatments are emphasized heavily in plans for landscape-restoration of southwestern forests (e.g., USDA FS 2011), and these activities could affect large areas of Mexican spotted owl habitat. Consequently, understanding how these treatments affect Mexican spotted owls is one of the major questions faced in integrating recovering this owl with plans for restoring southwestern forests. Although this has been clearly noted for years (e.g., USDI FWS 1995, Beier and Maschinski 2003, Ganey et al. 2011), no studies on this topic have been funded to date. Consequently, we can only extrapolate from the sparse data available on this topic resulting from studies of other subspecies of spotted owls, which we summarize below.

Meiman et al. (2003) conducted a case study of a single male northern spotted owl before, during, and after a commercial thinning operation conducted within the home range of this owl. Approximately 96 ha (237 ac) of forest lands were commercially thinned in this operation. Treatments occurred outside of a 28-ha (70-ac) designated core area, but within 70 m (230 ft) of nest trees used by the resident owls. Approximately 55 ha (136 ac) were thinned to a basal area of 39 m² ha⁻¹ (170 ft² ac⁻¹), a 4.5-ha (11.1-ac) area was thinned to 20.7 m² ha⁻¹ (90.2 ft² ac⁻¹) basal area, and a third area was thinned to 29.9 m² ha⁻¹ (130.2 ft² ac⁻¹). Breeding-season home-range size of the radio-marked male declined slightly following thinning (from 895 ha [2,212 ac] to 753 ha [1,861 ac]), but shifted geographically to exclude part of the thinned area and include unthinned areas elsewhere. In contrast, the non-breeding season home range was 2.3 times larger after harvest (2,825 ha [6,978 ac]) than before harvest (1,204 ha [2,974 ac]). The radio-marked owl was located up to 7 km (4.4 mi) from the nest area during the non-breeding season after thinning, versus 3.4 km (2.1 mi) before thinning. Size of core use areas did not differ significantly between pre- and post-harvest periods, but as with home range, geographic shifts were observed away from the thinned area. Based on number of locations, use of the thinned stand was significantly reduced after harvest. Thus, results suggest some spatial shifts in areas used following harvest, as well as reduced use of the thinned stand following harvest. However, results are difficult to interpret because we generally lack information about temporal variation in space and stand use. Further, this study is unlikely to shed much light on how restoration
treatments might affect Mexican spotted owls, because the residual basal areas in treated stands (20.7 to 39 m² ha⁻¹ [90.2 to 170 ft² ac⁻¹]) were far greater than residual basal areas typical of restoration projects in the southwestern U.S. (11.5 to 16.1 m² ha⁻¹ [50 to 70 ft² ac⁻¹]; USDA FS 2011:43)

Seamans and Gutiérrez (2007) examined the relationship between habitat selection of California spotted owls and variation in habitat in the Sierra Nevada. They modeled the probability of territory colonization, territory extirpation, and breeding dispersal in relation to the amount of mature forest within and among territories, and included a covariate to evaluate the effects of alteration of mature conifer forest habitat by timber harvest on these parameters. Estimates of habitat variables were based on 400-ha (988-ac) circles centered on the geometric center of all owl locations for a territory within a given year.

The probability of territory colonization was related to both area of mature conifer forest within a territory and alteration of that habitat. The top model for colonization indicated that territories in which ≥20 ha (49 ac) of mature conifer forest habitat was altered by timber harvest experienced a 2.5% decline in occupancy probability.

The top model for territory extirpation suggested that this parameter was negatively related to amount of mature forest within a territory. The structure of this top model did not allow them to separate the effects of habitat alteration within territories from variation in amount of mature forest among territories. Assuming that the variation in territory extirpation probability was due to variation in amount of mature conifer forest among territories, this model suggested that occupancy probability increased approximately 1.1% for every 20-ha difference in amount of mature conifer forest among territories.

The probability of breeding dispersal (i.e., leaving an established territory in year $t$ to move to another territory in year $t+1$) was related to both amount of mature conifer forest and alteration of that habitat. The top-ranked model suggested that probability of breeding dispersal was negatively related to the amount of mature conifer forest within a territory and positively related to alteration of ≥20 ha (49 ac) of mature conifer forest. This model also included an interaction between amount of mature conifer forest and alteration of that habitat. This interaction term suggested that breeding dispersal was much more likely to occur in territories with <150 ha (371 ac) of mature conifer forest that experienced habitat alteration than in territories with greater amounts of mature conifer forest that did not experience habitat alteration.

Seamans and Gutiérrez (2007) did not provide details on what types of treatments were involved in habitat alteration in this study, nor on spatial extent of those treatments. That is, they modeled a covariate based on alteration of ≥20 ha (49 ac) of mature mixed-conifer forest, but provided no information on how frequently territories experienced alteration of that magnitude versus larger areas. These limitations complicate interpretation of their results. Nevertheless, those results generally indicate positive effects of amounts of mature conifer forest and negative effects of alteration of ≥20 ha (49 ac) of mature conifer forest on demographic parameters.

Gallagher (2010; see also USDA FS 2010b) monitored movements and habitat use of 10 radio-marked California spotted owls in the northern Sierra Nevada in a landscape recently modified
by fuels treatments. Fuels treatments included: Defensible Fuel Profile Zones (DFPZs), understory thin, understory thin followed by underburn, and group selection. DFPZs were areas approximately 0.4 – 0.8 km (0.2 – 0.5 mi) wide where surface, ladder, and crown fuels loadings were reduced (USDA FS 2009). They were typically constructed along roads and ridge tops to reduce fuel continuity across the landscape and provide a defensible zone for fire suppression activities, and were designed to function effectively under 90th percentile weather conditions. Understory thin treatments allowed removal of trees <25.4 cm (10 in) in dbh. Understory thin with underburn allowed for use of surface fire following thinning. Group selection treatments allowed removal of all trees <76.2 cm (30 in) in patches <0.8 ha (2 ac) in area.

Radio-marked owls avoided DFPZs, but use of all other treatments was variable, and results were confounded by spatial orientation of treatments relative to owl core areas. Noting these complicating factors, Gallagher (2010:2) noted that “Conclusions from this study are exploratory and are intended to provide a baseline for further research.”

Dugger et al. (2011) evaluated relationships between northern spotted owls and barred owls in the southern Cascades of Oregon. They modeled the effects of barred owl presence on northern spotted owl territory occupancy, using amount of suitable spotted owl habitat as a covariate. Northern spotted owl territory colonization rates were strongly and negatively related to detections of barred owls, and territory extirpation rates were strongly and positively related to barred owl detections. Extirpation rates increased in response to decreased amounts of old forest habitat within territory cores, and colonization rates were greater where old forest habitat was less fragmented. Dugger et al. (2011) concluded that the combined barred owl and habitat effects observed suggested that interference competition was occurring between these owl species. They further concluded that these effects suggested that maintaining northern spotted owls on the landscape in the face of this competition would require conserving large amounts of contiguous old forest habitats.

As noted earlier, empirical data on effects of forest treatments on spotted owls are sparse and difficult to interpret. Although all of the studies discussed above individually present limits to interpretation, collectively they suggest that at least some kinds of mechanical forest treatments may negatively impact spotted owls. No clear guidance emerges from these studies relative to types, extents, or spatial arrangement of treatment that might minimize impacts to owls. Such information is badly needed if management is to proceed in owl habitat. Some treatments may have beneficial or neutral effects, but we do not know which types and intensities of treatments may be beneficial, neutral, or harmful. Lacking such information, managers should proceed cautiously in terms of treatment intensity and extent. That is, initial treatments should be limited in spatial extent and treatment intensity, and should be aimed at balancing reduced fire risk with maintaining the mature forest structure that seems to be favored by Mexican spotted owls. And all treatments in owl habitat should be linked to rigorous monitoring of owl response, to allow us to evaluate the effects of different types of treatments in an adaptive management context.

c. Grazing.—Heavy grazing intensity by domestic livestock and wild ungulates, repeated over successive seasons, can create a short to moderately long disturbance to vegetation that provides cover and food to the owl’s prey, and it can influence both tree regeneration and dynamics and composition of understory vegetation in forests occupied by owls. Based on distribution of prey
species and regional variation in the owl’s diet (e.g., Ward and Block 1995), portions of the owl’s range that are most susceptible to disturbance from heavy grazing include regions where Mexican spotted owls commonly consume voles, hunt near the edges of montane meadows allocated as key grazing areas, or where domestic livestock and wild ungulates are found grazing on forested slopes or in riparian habitats within canyons used by Mexican spotted owls.

Only one study has specifically addressed effects of grazing by domestic livestock on Mexican spotted owls. This study examined small mammal abundance and diversity in adjacent grazed and ungrazed transects in two owl territories in the canyonlands of southern Utah. Both woodrat abundance and overall small mammal species diversity were greater in ungrazed than in grazed transects (Willey and Willey 2010). There also is circumstantial evidence that grazing may affect prey abundance and thus indirectly affect owls. The primary evidence here comes from 1) studies on impacts of livestock on plant communities and the features of those communities that influence prey populations (described below under Prey Habitat), and 2) the influence of abundance of various prey species or groups of species on the owl’s feeding habits and reproduction (described below under Diet and Prey Selection, and Effects of Prey on Vital Rates). For example, species such as voles (and, to a lesser extent, woodrats) that are highly dependent on herbaceous plants for cover, food, and water are found in much lower abundance where drought combines with successive seasons of heavy grazing intensity, without opportunity for plant development and recovery from grazing events. 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, Ganey et al. 2011). Current evidence suggests that small mammal biomass (including voles and mice) influences Mexican spotted owl reproductive output (Ward 2001). Hence, grazing can negatively influence owl abundance indirectly by decreasing populations of key prey species.

Grazing also can also 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 bosqués in parts of their range (Bendire 1892, Bailey 1928, Phillips et al. 1964). Most of these areas have been heavily impacted by grazing, and there are no recent records of Mexican 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 more 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 between 1987 and 2007. He attributed much of this decline to increased browsing pressure by elk (*Cervus elaphus*). 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. Thus, this example documents an indirect effect on owl habitat involving grazing mediated by climate change. The observed changes in forest structure and composition were significant enough to cause the local extirpation of one formerly common bird species and severe population declines in several other species. Similar impacts may have occurred elsewhere in montane riparian systems.

d. 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. No studies have directly examined the effects of land development on Mexican spotted owls, so the extent of potential impacts remains largely unknown. Impacts may be significant, however. For example, 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-year period (Manley et al. 2009).

Development impacts may vary by area. For example, 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. Presumably, development impacts will be greater in landscapes with larger amounts of private land, although some forms of development may have greater impacts than others. Development impacts also may depend on spatial location. For example, 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 (see Landscape Connectivity, above) or wintering areas (see Seasonal Migration, below) 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 negatively impact habitat quality for Mexican spotted owls. For a broader discussion of types of development and potential impacts to Mexican spotted owls, see Part II.H.3.x.

e. 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. Unfortunately, the science on ecological effects of climate change is just beginning to emerge. Thus, most assessments of effects of climate change on the spotted owl are speculative and based on circumstantial information (but see Peery et al. 2011). The emerging phenomenon of climate change has the potential to impact Mexican spotted owls in three general ways:

- Directly, through impacts on key physiological processes like thermoregulation and water balance,
- Indirectly, through similar impacts on desired prey species, and
- Indirectly, by causing shifts in physical limits that control distribution of other animal or plant species that create biological communities that influence the owl (e.g., Martin 2007).
Mawdsley et al. (2009) discussed these effects 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 prey-predator relationships; and, 6) increased population or range expansion of species that are direct competitors. In this section, we discuss topics 1 and 2. Topics 3-6 are discussed below under Population Ecology.

1. Shifts in Distribution.—Shifts in Mexican spotted owl distribution could occur in response to predicted warming in the Southwest that may cause elevational and latitudinal shifts in tree species distribution. Predicted warming and drying in the Southwest may cause both latitudinal and elevational shifts in tree species distribution, as well as tree species extirpations at higher elevations (Dale et al. 2001, Mueller et al. 2005, DeGomez and Lenart 2006, Archer and Predick 2008). Over a long period of time the shift in plant communities could result in shifts in the distribution of both the owl and many of its important prey species. Exactly how these shifts will play out remains unknown, but some tree species and forest types currently present may be lost or greatly reduced in extent, especially where such species or communities occupy the upper elevations of island mountain ranges. For example, Mexican spotted owls occur in mixed-conifer and pine-oak forests at the tops of many of the Sky Island ranges in Arizona and New Mexico. Conifers within the Sky Islands of southern Arizona may be eliminated as temperatures increase and snowpack runoff decreases (Archer and Predick 2008). Loss of these forest types in these mountains presumably would eliminate or greatly reduce habitat for owls in these ranges. This in turn would greatly reduce landscape connectivity for Mexican spotted owls, likely reducing population viability as well (e.g., Keitt et al. 1995, 1997, Barrowclough et al. 2006, see also Ganey et al. 2008).

In contrast, however, these species also may migrate northward in response to changing climate, and/or Cordilleran (Rocky Mountain) species could be replaced by species with more Madrean affinities (such as Apache or Chihuahuan pines, or various species of evergreen oaks). We are aware of efforts to model and map shifting distributions of major southwestern conifers in relation to various climate-change scenarios, but results of these efforts have not yet been published. It seems likely, however, that loss of tree species or shrinkage in species’ range extent will outpace colonization by new species in the face of rapid climate change. Further, Mexican spotted owls frequently inhabit late-successional forests, and it will take considerable time for such forests to develop even if appropriate tree species are able to colonize new areas. Thus, at least in the short term, Mexican spotted owls likely will face reductions in habitat extent and greater fragmentation of suitable habitat within their current range. Such possible shifts in distribution of owl habitat argue for preserving management options in areas not currently occupied by Mexican spotted owls, but where climate and tree species distribution models predict that owl habitat could develop in the future.

2. Direct Loss of Habitat.—Mexican spotted owls also may experience direct loss of or alteration of habitat due to other climate-induced disturbances such as heat stress to plants, increased fire frequency, and insect outbreaks (e.g., Ayres and Lombardero 2000, Dale et
al. 2001, Breshears et al. 2009, Floyd et al. 2009, van Mantgem et al. 2009, Allen et al. 2010). For example, over multi-century periods, increased and decreased activity of spruce budworms coincided with wetter and drier periods, respectively (Swetnam and Lynch 1993, Ryerson et al. 2003), and bark beetle outbreaks have caused considerable tree mortality during a recent drought (e.g., Raffa et al. 2008, Negron et al. 2009, USDA FS 2009). Increasing levels of drought, along with associated insect outbreaks and wildland fires, could rapidly and dramatically affect the distribution, amount, and composition of Mexican spotted owl habitat. Finally, increasing temperatures may increase the prevalence of wildland fire, both alone and in concert with other disturbance agents such as insects and disease (e.g., Dale et al. 2001, McKenzie et al. 2004). How resilient owls and their habitats will be to these types of disturbances remains unknown.

5. Prey Ecology

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. This section provides information on the owl’s common prey species. Although the strong link between raptors and their food is well-documented (e.g., 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 (Noon and Franklin 2002).

A. Hunting Behavior

Forsman (1976) described spotted owls as “perch and pounce” predators. They typically locate prey from an elevated perch by sight or sound, then pounce on the prey and capture it with their talons. Spotted owls also have been observed capturing flying prey such as bats, birds, and insects (Verner et al. 1992, Duncan and Sidner 1990). They hunt primarily at night (Forsman et al. 1984, 2004; Ganey 1988), although infrequent diurnal foraging has been documented (Forsman et al. 1984, Laymon 1991, Sovern et al. 1994, Delaney et al. 1999a).

B. Diet and Prey Selection

Numerous studies have provided information on diets of Mexican spotted owls based on examination of prey remains from regurgitated pellets (see summary in Ward and Block 1995, also Wagner et al. 1982, Johnson 1997, Young et al. 1997, Willey 1998a, Seamans and Gutiérrez 1999, Ward 2001, Block et al. 2005, Bravo-Vinaja et al. 2005). Mexican spotted owls consume a variety of prey throughout their range, but they commonly eat small- and medium-sized rodents such as woodrats, mice, and microtine voles (Ward and Block 1995, Ganey et al. 2011). Mexican spotted owls also consume rabbits, bats, birds, reptiles, and insects.

The diet of Mexican spotted owls varies by geographic location (Ward and Block 1995: Fig. II.5.2). For example, woodrat consumption by Mexican spotted owls is far greater where owls occur in rocky canyons (e.g., southern Utah, Rinkevich 1991, Willey 1998a) than where owls occur in dense forests (e.g., the Sacramento Mountains, New Mexico; Ward 2001). In contrast, Mexican spotted owls occupying mountain ranges with forest-meadow interfaces take more voles than in other areas (Ganey 1992, Ward and Block 1995: Fig. II.5.2, Ward 2001). Regional
differences in the owl’s diet likely reflect geographic variation in prey abundance and habitats of both the owl and its prey. Forsman et al. (2001) documented similar spatial variation in a regional analysis of diets of northern spotted owls.

Ward and Block (1995) retrospectively examined the link between abundance or consumption of specific prey and successful reproduction by Mexican spotted owls in the Sacramento Mountains, New Mexico (BRE EMU). They were not able to demonstrate strong relationships, but fecundity of Mexican spotted owls in this region appeared to be most associated with trends in abundance of Peromyscid mice during the time period studied (Ward and Block 1995). Seamans and Gutiérrez (1999) also did not observe strong relationships between number of young produced and the proportion of biomass of any particular prey species consumed by Mexican spotted owls in two populations, one in northern Arizona and another in west-central New Mexico. As in other studies of this owl’s diet, small mammals comprised > 88% of dietary biomass, and, according to biomass consumed, woodrats were relatively important prey to owls in both populations (Seamans and Gutiérrez 1999).

The lack of demonstrated strong relationships in these studies does not mean that such relationships do not exist. More likely, it reflects difficulty in documenting the link between prey abundance and owl reproduction using opportunistic sampling of prey remains without knowledge of prey abundance or prey selection (i.e., the ratio between amounts in the owl’s diet and availability, Ward 2001:Chapter 3).

Ward (2001) expanded on the work in the Sacramento Mountains summarized in Ward and Block (1995), incorporating data from additional years. In this study, five species of rodents (deer mouse \([P. maniculatis]\), brush mouse \([P. boylii]\), Mogollon vole \([M. mogollonensis]\), long-tailed vole \([M. longicaudus]\), and Mexican woodrat \([N. mexicana]\)) provided from 53 to 77% of the diet by frequency and from 41 to 66% of the diet by biomass over a six-year period (1991 to 1996). Mean number of Mexican spotted owl young produced annually over this period was most strongly correlated with the combined available biomass of mice and voles. More intriguing was that consumption of woodrats was proportionally lower in the Sacramento Mountains owl population than in seven other populations of spotted owls that were studied, and temporal variability in owl reproduction was inversely related to the proportion of woodrats in the diet across these eight populations (Ward 2001: Fig. 4.7). Based on this finding, and the dominance of woodrats in the diet throughout much of the owl’s range, Ward (2001) suggested that woodrats likely were an important prey type for spotted owls in many geographic areas.

In rocky-canyon habitats in southern Utah, Willey and Willey (2010) examined prey abundance and owl diet composition within three owl territories. Owl diets were dominated (>80% of biomass consumed) by woodrats in this area. The first years of this study (2000 to 2003) coincided with a period of severe drought, followed by significant increases in local precipitation from 2004 to 2006. Rodent populations on three trapping grids showed strong increases in species richness and abundance during increasingly wetter study years. Mexican spotted owl reproduction was low during the 2000 to 2003 dry period, and by 2003 only male spotted owls were detected at the sites. All three sites were re-colonized by female spotted owls during the period of increased precipitation from 2004 to 2006, and reproduction increased during this period. This study was observational and did not necessarily document cause-and-effect
relationships, and inference is limited by small sample size. Nonetheless, results suggested that precipitation influenced site occupancy and reproductive rates of Mexican spotted owls indirectly by increasing prey abundance (Willey and Willey 2010).

C. Prey Habitat

Understanding habitat relationships of important prey species can provide additional information relative to foraging behavior and ecology of a predator. Habitat correlates of the owl’s common prey indicate that each prey species uses unique microhabitat features (Ward and Block 1995, Sureda and Morrison 1998, 1999, Ward 2001, Block et al. 2005) and that these features may vary among vegetation types (Sureda and Morrison 1999). In general, deer mice appear relatively ubiquitous in distribution, occupying areas with variable conditions, whereas brush mice are more restricted to communities with a strong oak component and dry, rocky substrates with sparse tree cover (Block et al. 2005). Mexican woodrats typically occur in areas with considerable shrub or understory tree cover, low grass cover, high volumes of large logs, and/or presence of rock outcrops (Sureda and Morrison 1998, 1999, Ward 2001, Block et al. 2005). In the canyonlands of southern Utah, Mexican woodrats were captured only in rocky canyons (Sureda and Morrison 1998, 1999), where radio-marked owls concentrated foraging activity (Willey and van Riper 2007). Mogollon voles occur in areas with high herbaceous cover, primarily grasses, and long-tailed voles are associated with high herbaceous cover, primarily forbs, many shrubs, and limited tree cover (Ward 2001). Thus, to provide a diverse prey base, managers can provide a diversity of habitats for prey species when designating PAC boundaries or manipulating vegetative conditions in recovery habitat. Managing habitat for a diversity of prey species may help buffer against population fluctuations of individual prey species and provide a more constant food supply for the owl (Sureda and Morrison 1998, Ward 2001, Block et al. 2005).

Ward (2001) suggested that longer-term (50-year) management aimed at increasing late-seral conditions of mixed conifer forest should favor increased abundance of woodrats, and that increasing woodrat abundance would be more successful for recovering Mexican spotted owl populations than management aimed at increasing abundance of mice. This conclusion was based on the demonstrated inverse association between consumption of woodrats and temporal variability in the owl’s reproduction across eight populations of spotted owls (Ward 2001: Fig. 4.7). Given the relationships among key habitat variables and common prey abundance, shorter term management also should include fostering good to excellent conditions in key grazing areas (e.g., montane meadows) to ensure adequate vole populations near and within owl foraging areas. Of the common prey species examined, mice were considered less manageable because their abundances were correlated with habitat attributes that were much more difficult to manipulate (e.g., seed mast and rocky slopes; Ward 2001: Chapter 2). In contrast, vole numbers likely could be increased by managing for increased cover and height of grasses and forbs (Ward 2001), and woodrat numbers might be increased by promoting shrub diversity and increasing cover of large logs (Sureda and Morrison 1999, Ward 2001, Block et al. 2005). Because microhabitat features associated with small mammal species can vary among geographic regions and habitats within regions (Ward and Block 1995, Sureda and Morrison 1999, Block et al. 2005), management for small mammals may require site- or at least habitat-specific knowledge about relationships between mammal abundance and habitat features.
Habitat conditions for the owl’s prey, access to those prey, and abundance of these prey species can also be changed by fire. Indeed, differences among areas in composition of prey communities may at least partially explain the apparent inconsistent response of spotted owls to fire (discussed above). To date, adequate long-term studies of small mammal populations have not been conducted to determine effects of fire on many of the owl’s prey species. Results of short-term studies suggest that individual small mammal species respond differently to fire, and that small mammal response is driven more by remnant understory composition and response than by fire severity itself (Kyle and Block 2000, Converse et al. 2006a, 2006b, 2006c), although severity can strongly influence understory composition.

6. Population Ecology

Knowing how and why populations change over time is a fundamental requisite for forecasting and developing strategies for species recovery. The change in size of any population during a specified time period can be represented with the simple equation,

\[ N_{t+1} = N_t - D_t + B_t + I_t - E_t \]

where \( N_t \) is the population size at time \( t \), \( D_t \) is the number of individuals dying, \( B_t \) is the number of new individuals produced in the population (births), \( I_t \) is the number of individuals immigrating into the population, and \( E_t \) is the number of individuals emigrating from the population. The combined effect of births, deaths, immigrations, and emigrations dictate the viability of the population, and hence its long-term persistence. Three of these parameters for Mexican spotted owl populations, abundance, survival, and reproduction, are discussed below in greater detail. Knowledge regarding immigration or emigration is provided under the topic of dispersal because of the importance of inter-population movements to metapopulation structure and persistence.

A. Abundance

a. Density.—The number of individuals in a population (or population size, \( N \)) divided by the area used by those individuals is known as density. The most reliable estimates of Mexican spotted owl density come from mark-resighting data analyzed with closed-population estimators (e.g., Pollock et al. 1990). These procedures provide for estimating the probability of detecting individual owls and ultimately for correcting the sample count of owls to more truly reflect population size. Unfortunately, only one study has been implemented for the primary purpose of estimating density of Mexican spotted owls, and that study, although geographically extensive, was limited to a single year. By surveying and marking owls in a stratified-random set of 25 quadrats across the UGM EMU (range in quadrat size = 43.7 to 76.4 km²), Ganey et al. (2004) estimated that 2,941 (Coefficient of Variation = 36.6%) territorial adult or subadult owls occupied this EMU (excluding tribal lands, which were not included in the sampling frame). Density of adult and subadult owls within individual quadrats ranged from 0 to 0.44 territorial owls km⁻².

Using a different study design, Seamans et al. (1999) reported from 0.026 to 0.075 territorial females km⁻² in a 585-km² area in northern Arizona and from 0.055 to 0.099 owls km⁻² in a 323-km² area in west-central New Mexico from 1991 to 1997 (densities calculated from data in their Fig. 1). Density of territorial females was consistently greater in the New Mexico population.
during this period. The study area in Arizona included large areas of ponderosa pine and ponderosa pine-Gambel oak forest interspersed among mixed-conifer forests, whereas the study area in New Mexico was dominated by mixed-conifer forest. Seamans et al. (1999) suggested that the greater density of Mexican spotted owls in the New Mexico study area was a function of the greater relative amount of mixed-conifer forest found in that study area.

Two other studies have used sample counts within fixed quadrat areas without estimating detection probabilities (Skaggs and Raitt 1988, 1995, Young et al. 1998). These probabilities are required for correcting raw counts of owls for individuals that were actually present but never detected. Ward et al. (1995) reanalyzed data from Skaggs and Raitt (1988) for the Sacramento Mountains, New Mexico. They reported mean densities of 0.275 owls km\(^{-2}\) in quadrats dominated by mixed-conifer forest, 0.080 owls km\(^{-2}\) in quadrats dominated by ponderosa pine forest, and 0.022 owls km\(^{-2}\) in quadrats dominated by pinyon-juniper woodland. These results demonstrate variation in abundance among areas that differ in habitat composition without the confounding variation associated with time (all quadrats were surveyed in one year).

Young et al. (1998) reported densities for five randomly selected 70-km\(^{2}\) quadrats surveyed in Chihuahua Mexico. The counts of territorial owls ranged from 0.055 to 0.111 owls km\(^{-2}\) in the five quadrats. Vegetation composition was not described for individual quadrats but 71\% of the overall area surveyed consisted of pine-oak forest, with pure pine and mixed-conifer forest comprising 17\% and 12\% of total area, respectively.

Densities of Mexican spotted owls in canyonlands have yet to be reported. As a reference point for estimates reported above, density of northern spotted owls in a study area containing large core areas of late-seral mixed-evergreen forest (perceived to be relatively high-quality habitat for these owls; Franklin et al. 2000) was 0.272 owls km\(^{-2}\) in 1993 (Franklin unpubl. data cited in Ward and Block 1995). Caution must be exercised in comparing densities among study types and different sized sampling areas, however. Size and shape of the bounded area can influence the calculation of density in small study areas (Franklin et al. 1990), and if simple counts are not corrected by detection probabilities, results are further confounded if those probabilities differ between/among areas. But collectively, the above studies suggest that mixed-conifer forests support higher densities of Mexican spotted owls than areas dominated by other vegetation communities.

To date, three factors have been associated with Mexican spotted owl density. These include vegetation composition (discussed above), the degree of topographic relief (greater relief corresponds to greater density; Ganey et al. 2004), and fecundity from two years prior to a given density estimate (higher fecundity results in greater density in subsequent years; Seamans et al. 1999). These factors 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 et al. (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 (see Environmental Variation and Vital Rates).
b. Temporal Population Trends.—A fundamental parameter that describes population change is lambda (λ) or annual (finite) rate of population growth. Population trends can be shown as plots of density or population size over time and quantified as the average change in population size or mean λ during that period. Only a single study (Seamans et al. 1999, updated in Gutiérrez et al. 2003) has been conducted long and effectively enough to quantify trends in Mexican spotted owl abundance and population change.

Based on estimates of vital rates and a Leslie stage-projection matrix model, Seamans et al. (1999) reported declining populations for two study areas in Arizona and New Mexico. Although the years covered by these estimates were not stated explicitly, the declining trends were supported by estimates of annual abundance-based counts of owls from 1992 to 1997 (Seamans et al. 1999: Fig. 4). Gutiérrez et al. (2003) updated information on estimated trends in owl numbers (λ) for these study areas from 1993 to 2000. In the Arizona study area, mean λ (0.995, 95% confidence interval = 0.836–1.155) indicated a stable population (i.e., λ ≈ 1) over this period. In contrast, the population of Mexican spotted owls from the New Mexico study area appeared to be declining (i.e., λ < 1) by approximately 6% per year during this period (mean λ = 0.937, 95% confidence interval = 0.895–0.979). However, analytical methods used in Gutiérrez et al. (2003) differed between study areas and differed from the methods used by Seamans et al. (1999). These differences in methods complicate interpretation of the difference in observed trends between study areas and/or time periods.

Gutiérrez et al. (2003) also provided point estimates of “realized change.” This measure uses consecutive annual estimates of λ to estimate the proportion of the initial population remaining in a given year, yielding a parameter that is more easily interpreted than λ (Franklin et al. 2004). They estimated that the owl populations remaining in their Arizona and New Mexico study areas in the year 2000 were 69.1 and 60.8% as large, respectively, as the 1993 populations. In other words, they estimated declines of >30% in both populations from 1993 (the first year in which they could estimate λ) to 2000.

Stacey and Peery (2002, see also Stacey 2010: Table 35.1) also reported declining trends in owl populations in the Black Range and Zuni, San Mateo, and Magdalena Mountains, New Mexico, based on data from 1991 to 1999. Declining trends were evident in all ranges studied, as well as when populations from these ranges were combined for an overall analysis (overall λ = 0.803, 95% confidence interval = 0.73 to 0.89). 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). Stacey (2010:615-616) also suggested that earlier (probably prior to 1994) local extirpations occurred in the Sandia and Manzano Mountains, and possibly in the Datil and LaDrónnes Mountains, New Mexico. Seamans and Gutiérrez (2006; see also Seamans and Gutiérrez 2007 for effect of mates on breeding dispersal) suggested that spotted owls may use presence of conspecifics as cues in settling and therefore may be slow to re-colonize areas where they are locally extirpated (or even greatly reduced in number).

c. Temporal Trends in Occupied Sites.—Depending on the nature of the sampling design, time trends in the number or proportion of sites occupied in a study area can provide a surrogate index for trends in population numbers (MacKenzie et al. 2003). However, studies of site occupancy
through time that do not survey enough area to allow for detecting newly colonized or re-colonized sites will always show a decline.

There have been four studies that provided trends in number or proportion of sites occupied by Mexican spotted owls that may also be indicative of population trends. Johnson (2000) reported on occupancy of Mexican spotted owl territories in the Jemez Mountains, New Mexico from 1979 to 2000, with more formal monitoring conducted since 1989. Number of territories included in these annual estimates varied among years (maximum number in a year was 28 territories; average number monitored since 1989 was 20 territories), as did methods (e.g., early estimates were based on passive listening surveys rather than calling surveys). Results suggest that occupancy rates declined from 1985 to 1989 and have been fairly stable since 1989 (Johnson 2000: Fig. 1). Declines may have occurred earlier than 1985, but the change in methods makes it difficult to tell. By 2000, 14 of the 28 territories were known to be occupied by at least one Mexican spotted owl and eight of those territories were occupied by pairs.

Using a retrospective analysis of survey data gathered in the Sacramento Mountains of southern New Mexico, Lavier (2006) estimated the proportion of sites occupied by Mexican spotted owls following procedures recommended in the population monitoring section of this Recovery Plan. These procedures (see also MacKenzie et al. 2003) enhance estimation of site occupancy by also estimating and incorporating probabilities that owls are detected. Lavier’s (2006) study showed a dynamic but generally stable or slightly declining pattern of site occupancy by territorial owl-pairs in the Sacramento Mountains from 1989 to 2004. Estimated site occupancy by pairs in this population ranged from a high of 85.4% (SE = 0.03%) in 1992 to a low of 54.4% (SE = 0.05%) in 2000. Site occupancy was estimated at 71.0% (SE = 0.05) in 2004, the last year of the study.

In rocky-canyon habitats in southern Utah, Willey (2010) and Hockenbary (2011) conducted occupancy based surveys for Mexican spotted owls at 47 historic territories in Zion and Capitol Reef National Parks, Grand Staircase-Escalante National Monument, and on Cedar Mesa (BLM) from 2007-2009, following methods in MacKenzie et al. (2003). Willey (2010) classified owl territories as occurring either in xeric (Grand-Staircase and Capitol Reef) or mesic (Zion and Cedar Mesa) canyon habitat. Mesic sites included patches of mixed-conifer and riparian forest, whereas xeric sites were dominated by desert scrub vegetation. Estimated year one site occupancy at territories was 92% (SE = 0.075%) at the mesic sites and 47% (SE = 0.10%) at xeric sites. AIC-based selection of models of occupancy rate supported a model with detection probability constant across years and a strong habitat effect indicating that occupancy rates differed between mesic and xeric territories. Re-colonization rates also differed between habitats, with re-colonization rates more than twice as great at mesic territories, compared to xeric territories. Thus, Zion and Cedar Mesa populations experienced high occupancy and re-colonization rates, whereas the xeric study sites showed low rates of occupancy and re-colonization. Numerous additional xeric sites located in Capitol Reef and the Paria River that were occupied during the 1990s (Willey 1998, 2007) were no longer occupied during surveys conducted during 2007 and 2008, suggesting that populations in xeric locations may have declined in southern Utah.

Investigating the same study areas and 47 territories studied by Willey (2010), Hockenbary (2011) continued occupancy-based research, and studied relationships among recreation use-
level by humans, habitat covariates, and owl site occupancy, colonization, extirpation, and detection probabilities. Detection probability, as by the best model evaluated, was 0.89 (95% CI = 0.82 – 0.94) across all three years of study. Two competing models of occupancy, colonization, and extinction rates both included a site-specific mesic/xeric habitat covariate. These models outranked models that included effects of recreation. From the best approximating model, occupancy was estimated as 0.75 (95% CI = 0.57 - 0.87) and 0.50 (95% CI = 0.27 – 0.73) for mesic and xeric sites, respectively. Recolonization rate was estimated at 0.10 (95% CI = 0.02 – 0.37) for xeric sites and 0.53 (95% CI = 0.28 – 0.76) for mesic sites, and extirpation rate was constant across years (0.25; 95% CI = 0.15 – 0.39). The results did not support recreation effects on site occupancy or colonization and extinction rates. High recreation sites were occupied by Mexican spotted owls during each year of the study, and fledglings were observed in these sites multiple years. Thus, results suggest that current management practices and imposed limits to recreational activity in the study areas have been adequate for protecting spotted owls.

Similar to Willey (2010), Hockenbary (2011) estimated higher occupancy and recolonization rates and lower extirpation rates for mesic than for xeric sites, suggesting that mesic sites were more stable (i.e., constant occupancy) than xeric sites. He concluded that mesic habitats may have more favorable microclimates and habitat structure, roost and nest sites, and diverse habitats for the owl’s prey.

In summary, data on trends in populations or occupancy rates are sparse, and methods and sample sizes differ among studies, making comparisons difficult. In general, however, results suggest that most populations of Mexican spotted owls studied either have declined in the recent past or are still declining. Further, some evidence suggests that owls may be slow to re-colonize areas where such declines have occurred (Seamans and Gutiérrez 2006, Stacey 2010, Willey and Willey 2010).

B. Life History Strategy

In general, the life history of the Mexican spotted owl appears similar to those of the better-known northern and California subspecies. All three subspecies are characterized by high and reasonably constant adult survival rates, low juvenile survival rates, and relatively low and highly variable reproductive rates (e.g., Noon et al. 1992, Franklin et al. 2000, 2004, Blakesley et al. 2001, Gutiérrez et al. 2003, LaHaye et al. 2004, Anthony et al. 2006). These life history characteristics allow owls to reproduce when conditions are favorable and to survive unfavorable periods with little or no reproduction, a strategy that has been coined “bet-hedging” (e.g., Boyce 1988, Franklin et al. 2000).

Despite the above similarities, the Mexican spotted owl differs from the other two subspecies in important respects. In northern and California spotted owls, the population appears to contain numbers of non-territorial “floaters” (Franklin et al. 2000, 2004; Franklin. 2001). 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 Mexican spotted owl populations. 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 subset of the population that is
unable to find vacant territories. As a result, population trend tracks changes in reproduction with a short time lag (Seamans et al. 1999, Gutiérrez et al. 2003). Because reproduction in this owl is inherently variable (see Reproductive Biology and Rates, below), 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, which also are inherently variable within the range of the Mexican spotted owl.

C. Reproductive Biology and Rates

Like many temperate-zone *Strix* owls, Mexican spotted owls form a monogamous pair-bond. The reproductive process is opportunistic, and success is dependent in part on the physiological condition of the female and availability of prey (Hirons 1985, Gutiérrez et al. 1995). The typical chronology for successful reproduction entails: 1) reformation of the pair bond, courtship and nest selection, copulation; 2) egg-laying, incubation, and brooding of young (all referred to as nesting); and, finally, 3) rearing of young outside of the nest.

Knowledge of the annual reproductive cycle of the Mexican spotted owl is important both in an ecological context and for placing seasonal restrictions on management or other activities that may occur within areas occupied by Mexican spotted owls to minimize disturbance to nesting owls. In Arizona, courtship begins in March with pairs roosting together during the day and calling to each other at dusk (Ganey 1988). Eggs typically are laid from late-March to mid-April. Incubation begins shortly after the first egg is laid and lasts approximately 30 days. Only the female incubates the eggs. During incubation and the first half of the brooding period, the female leaves the nest only to defecate, regurgitate pellets, or receive prey delivered by the male, who does most or all of the foraging (Forsman et al. 1984, Ganey 1988, Delaney et al. 1999a). This chronology may vary slightly throughout the range of the owl and from year to year, depending on weather conditions during winter and spring.

Mexican spotted owls nest on cliff ledges, stick nests built by other birds, debris platforms in trees, and in tree cavities (e.g., Ganey and Dick 1995, Gutiérrez et al. 1995, Seamans and Gutiérrez 1995, Johnson 1997, Willey 1998a, May et al. 2004). Spotted owls have one of the lowest clutch sizes among North American owls (Johnsgard 1988, Gutiérrez et al. 1995). Females normally lay one to three eggs, two being most common, and four being observed rarely (LaHaye 1997, Gutiérrez et al. 2003). Re-nesting following nest failure is unusual but has been observed in Mexican spotted owls (Kroel and Zwank 1992, Gutiérrez et al. 1995).

The eggs usually hatch in early- to mid-May (Ganey 1988). Female spotted owls brood their young almost constantly for the first couple of weeks after the eggs hatch but then begin to spend time hunting at night, leaving the owlets unattended for up to several hours (Eric Forsman, FS, pers. comm., Delaney et al. 1999a). Nestling owls generally fledge from early- to late-June, roughly four to five weeks after hatching (Ganey 1988). Owlets usually leave the nest before they can fly, jumping from the nest to surrounding tree branches or the ground (Forsman et al. 1984, Ganey 1988). Owlets that end up on the ground often will climb, using talons and bill, up an understory tree to a safe roost site. The mobility and foraging skills of owlets improve gradually during the summer. Within a week after leaving the nest, most owlets can make short, clumsy gliding flights between trees. Three weeks after leaving the nest, owlets can sustain
flapping flight and hold and tear up prey on their own (Forsman et al. 1984). Fledglings depend on their parents for food during the early portion of the fledgling period. Hungry owlets give a persistent, raspy “begging call,” especially when adults appear with food or call nearby (Forsman et al. 1984, Ganey 1988). Begging behavior declines in late August, but may continue at low levels until dispersal occurs, usually from mid-September to early October (Arsenault et al. 1997, Ganey et al. 1998, Willey and van Riper 2000).

Mexican spotted owls breed sporadically and do not nest every year (Ganey 1988, Gutiérrez et al. 1995, 2003, White et al. 1995). In good years, much of the population will nest, whereas in some years only a small proportion of pairs will nest successfully (Fletcher and Hollis 1994, Gutiérrez et al. 1995, 2003). For example, during 12 years of study in Arizona and New Mexico (Gutiérrez et al. 2003), 63.6% of owl pairs nested in a given year, on average (SE = 8.91; range = 9.1 to 100%, n = 19 to 45 owl pairs monitored per year), and 74.6% of those pairs nesting fledged young (SE = 8.61, range = 0 - 100%). 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 (see Environmental Variation and Vital Rates, below).
Table B.5. Summary of estimates of reproductive output (young fledged per pair) of spotted owls.

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Age-class¹</th>
<th>Area</th>
<th>Populations studied²</th>
<th>Number of years³</th>
<th>Reproductive output</th>
<th>Source⁴</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mexican A, SA</td>
<td>A, SA</td>
<td>Arizona</td>
<td>1</td>
<td>12</td>
<td>0.929</td>
<td>0.188</td>
</tr>
<tr>
<td>Mexican A, SA</td>
<td>A, SA</td>
<td>New Mexico</td>
<td>1</td>
<td>12</td>
<td>0.702</td>
<td>0.199</td>
</tr>
<tr>
<td>Mexican A, SA</td>
<td>A, SA</td>
<td>New Mexico</td>
<td>1</td>
<td>6</td>
<td>0.72</td>
<td>0.631</td>
</tr>
<tr>
<td>Mexican A</td>
<td>A</td>
<td>New Mexico</td>
<td>4</td>
<td>NA</td>
<td>0.359</td>
<td>0.057</td>
</tr>
<tr>
<td>Mexican SA</td>
<td>A</td>
<td>New Mexico</td>
<td>4</td>
<td>NA</td>
<td>0.150</td>
<td>0.107</td>
</tr>
<tr>
<td>Mexican A, SA</td>
<td>A, SA</td>
<td>New Mexico</td>
<td>1</td>
<td>18</td>
<td>0.97</td>
<td>No estimate</td>
</tr>
<tr>
<td>Northern SA1</td>
<td>A</td>
<td>Rangewide</td>
<td>14</td>
<td>14</td>
<td>0.148</td>
<td>0.0584</td>
</tr>
<tr>
<td>Northern SA2</td>
<td>A</td>
<td>Rangewide</td>
<td>14</td>
<td>14</td>
<td>0.416</td>
<td>0.064</td>
</tr>
<tr>
<td>Northern A</td>
<td>A</td>
<td>Rangewide</td>
<td>14</td>
<td>14</td>
<td>0.744</td>
<td>0.058</td>
</tr>
<tr>
<td>California A, SA</td>
<td>A, SA</td>
<td>Rangewide</td>
<td>5</td>
<td>14</td>
<td>0.57-0.81⁵</td>
<td>0.16-0.82⁵</td>
</tr>
<tr>
<td>California A</td>
<td>A</td>
<td>Southern</td>
<td>1</td>
<td>12</td>
<td>0.345</td>
<td>0.028</td>
</tr>
<tr>
<td>California SA</td>
<td>A</td>
<td>Southern</td>
<td>1</td>
<td>12</td>
<td>0.139</td>
<td>0.050</td>
</tr>
</tbody>
</table>

¹ Age classes: A = adult, SA = subadult (first and second-year subadults combined), SA1 = first-year subadult, SA2 = second-year subadult. A, SA indicates that reproductive output was estimated for adult and subadult owls combined.
² Number of distinct study areas covered by estimate.
³ Number of years included in the study. NA = number not available.
⁴ Source: 1 = Gutiérrez et al. (2003); 2 = calculated from data in Ward (2001:Fig. 3.8); 3 = Stacey and Peery (unpubl. data); 4 = Johnson (2000); 5 = recalculated from fecundity in Anthony et al. (2006:Table 5); 6 = recalculated from fecundity in Franklin et al. (2004:Table 9); 7 = LaHaye et al. (2004).
⁵ Range across populations.
Annual reproductive output of Mexican spotted owls, defined as the number of young fledged per pair, varies both spatially, temporally, and by age-class (Seamans et al. 1999, Johnson 2000, Ward 2001, Gutiérrez et al. 2003, Stacey 2010). Fecundity, the number of female offspring produced per female in a population, is half of the value for reproductive output when the sex ratio in the offspring is 50:50. Similar to other spotted owl subspecies, average reproductive rates are generally low in Mexican spotted owl populations (Table B.5) and rarely exceed 1 young per pair per year, although higher rates may occur in some years (Ward 2001). However, average annual reproductive output in Mexican spotted owl populations can be as great as 1.4 young per pair (Ward 2001). Although all three subspecies of spotted owls exhibit temporal fluctuations in reproductive success, the amplitude of those fluctuations is generally greatest for the Mexican spotted owl (Ward 2001: Fig. 4.7; see also reviews in White et al. 1995, Burnham et al. 1996, Franklin et al. 2004; Anthony et al. 2006). Adult individuals usually have higher reproductive rates than subadults (Table B.5).

D. 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 and documenting their presence through re-sighting in a spatially explicit population through multiple years (e.g., Forsman et al. 1996), or by intensively monitoring fates of radio-marked owls over shorter periods of time.

Gutiérrez et al. (2003) estimated apparent annual survival rates of Mexican spotted owls over a 10-year period on two study areas in Arizona and New Mexico, using mark-resighting methodology. Estimates of adult survival were comparable to estimates derived using similar methods for northern (Anthony et al. 2006) and California (Franklin et al. 2004) spotted owls, and to estimates from radio-marked owls (Table B.6). In contrast, estimates from four other populations in New Mexico were slightly lower (Table B.6, Stacey and Peery unpubl. data). Mark-resighting estimates of survival may be biased low if owls in these age classes emigrate from study areas (Zimmerman et al. 2007). Such emigration does not appear to be common, but Gutiérrez et al. (1996) reported one long-distance movement that may represent an example of adult dispersal, Arsenault et al. (1997) noted apparent subadult dispersal in Mexican spotted owls, and Duncan and Speich (2002) reported instances of “temporary and permanent emigration in response to fire altered habitat.” Survival rates based on monitoring of radio-marked owls also could be underestimated if radios affect survival. Evidence on whether or not radios or their attachment affect survival of spotted owls is equivocal (e.g., Paton et al. 1991, Foster et al. 1992).

Estimates of juvenile survival rates are considerably lower and more variable than estimates for adult survival (Table B.6). Mark-recapture estimates of juvenile survival could be biased low if 1) substantial numbers of owls emigrate from the study area, or 2) a lag of several years occurs before marked juveniles reappear as territory holders, at which point they are first detected for recapture (White et al. 1995). As in all spotted owl subspecies, juvenile Mexican spotted owls have a high dispersal capability (Arsenault et al. 1997, Ganey et al. 1998, Willey and van Riper 2000). Consequently, a substantial portion of marked juveniles may emigrate from the study
Table B.6. Summary of estimates of annual survival for spotted owls.

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Age-class1</th>
<th>Sex2</th>
<th>Area</th>
<th>Populations studied3</th>
<th>Methodology4</th>
<th>Survival estimate</th>
<th>Source 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mexican</td>
<td>A, SA</td>
<td>B</td>
<td>Arizona</td>
<td>1</td>
<td>M-R</td>
<td>0.856</td>
<td>1</td>
</tr>
<tr>
<td>Mexican</td>
<td>A, SA</td>
<td>B</td>
<td>New Mexico</td>
<td>1</td>
<td>M-R</td>
<td>0.859</td>
<td>1</td>
</tr>
<tr>
<td>Mexican</td>
<td>A, SA</td>
<td>F</td>
<td>Rangewide</td>
<td>Several</td>
<td>RT</td>
<td>0.806</td>
<td>2</td>
</tr>
<tr>
<td>Mexican</td>
<td>A, SA</td>
<td>M</td>
<td>Rangewide</td>
<td>Several</td>
<td>RT</td>
<td>0.799</td>
<td>2</td>
</tr>
<tr>
<td>Mexican</td>
<td>A</td>
<td>B</td>
<td>New Mexico</td>
<td>4</td>
<td>M-R</td>
<td>0.769</td>
<td>3</td>
</tr>
<tr>
<td>Mexican</td>
<td>A</td>
<td>B</td>
<td>Rangewide</td>
<td>14</td>
<td>M-R</td>
<td>0.750-0.886</td>
<td>4</td>
</tr>
<tr>
<td>Mexican</td>
<td>A</td>
<td>B</td>
<td>Rangewide</td>
<td>14</td>
<td>M-R</td>
<td>0.415-0.860</td>
<td>4</td>
</tr>
<tr>
<td>Northern</td>
<td>A</td>
<td>B</td>
<td>Rangewide</td>
<td>14</td>
<td>M-R</td>
<td>0.626-0.886</td>
<td>4</td>
</tr>
<tr>
<td>Northern</td>
<td>J</td>
<td>B</td>
<td>Arizona</td>
<td>1</td>
<td>M-R</td>
<td>0.230</td>
<td>9</td>
</tr>
<tr>
<td>Mexican</td>
<td>J</td>
<td>B</td>
<td>New Mexico</td>
<td>1</td>
<td>M-R</td>
<td>0.080</td>
<td>1</td>
</tr>
<tr>
<td>Mexican</td>
<td>J</td>
<td>B</td>
<td>Arizona</td>
<td>1</td>
<td>RT</td>
<td>0.205-0.287</td>
<td>6</td>
</tr>
<tr>
<td>Mexican</td>
<td>J</td>
<td>B</td>
<td>Utah</td>
<td>1</td>
<td>RT</td>
<td>0.096</td>
<td>7</td>
</tr>
<tr>
<td>Northern</td>
<td>J</td>
<td>B</td>
<td>Rangewide</td>
<td>11</td>
<td>M-R</td>
<td>0.258</td>
<td>8</td>
</tr>
<tr>
<td>California</td>
<td>J</td>
<td>B</td>
<td>Southern</td>
<td>1</td>
<td>M-R</td>
<td>0.296</td>
<td>9</td>
</tr>
</tbody>
</table>

1 Age classes: A = adult, SA = subadult, and J = juvenile. A, SA indicates that survival was estimated for adult and subadult owls combined.
2 F = female, M = male, B= survival estimated for both sexes combined.
3 Number of distinct study areas covered by estimate.
4 Methodology underlying survival estimate. M-R = mark – recapture; RT = radio-telemetry.
5 Source: 1 = Gutiérrez et al. (2003); 2 = White et al. (1995:Table 2.4); 3 = Stacey and Peery (unpubl. data); 4 = Anthony et al. (2006: Table 13); 5 = Franklin et al. (2004); 6 = Ganey et al. (1998); 7 = calculated from data in Willey and van Riper (2000); 8 = Burnham et al. (1996); 9 = LaHaye (pers. comm. in Noon et al. [1992:Table 4; San Bernardino Mountains]).
6 Range across populations studied.
7 Estimate differed depending on whether or not owls that were suspected to be dead were included as fatality events or censored.
areas. This may explain why the apparent survival of juveniles was lower for the smaller New Mexico study area than for the larger Arizona study. Concerning the second point, available data (see Dispersal, below) indicates that most Mexican spotted owls settle in the first three years of life, suggesting that a bias in survival estimates caused by time lag in detection may not be large.

Estimates from radio-telemetry studies also suggested low juvenile survival rates (Ganey et al. 1998, Willey and van Riper 2000). Biases in radio-telemetry estimates of juvenile survival can result if radios significantly affect their survival, or if these studies were conducted during time periods with lower than usual survival (e.g., a period of low prey availability). As noted above, evidence for effects of radios on survival of spotted owls is equivocal (Paton et al. 1991, Foster et al. 1992). However, at least one of the radio-telemetry studies (Ganey et al. 1998) may have occurred during a period generally unfavorable for owls. Seamans et al. (1999) estimated fecundity and survival rates of owls over a seven-year period in two study areas, one of which overlapped with the study area in Ganey et al. (1998). The two years in which radio-marked juveniles were studied (1994 and 1995; Ganey et al. 1998) also had the lowest fecundity estimates within that seven-year period in both study areas (Seamans et al. 1999: Fig. 2), and two of the three lowest estimates of adult survival (Seamans et al. 1999: Fig. 3). Similarly, the two years of the juvenile dispersal study conducted by Ganey et al. (1998) corresponded with the lowest recruitment rates estimated by Gutiérrez et al. (2003: Fig. 7a) in their Arizona study area. Collectively, these findings suggest a generally unfavorable period for owls. As a result, estimated survival rates may not be representative of survival rates during more favorable periods.

In summary, considerable uncertainty exists concerning survival rates of Mexican spotted owls, and especially concerning juvenile survival rates. Despite that uncertainty, the available estimates are useful as qualitative descriptors of the life-history characteristics of Mexican spotted owls. Accordingly, Mexican spotted owls exhibit high adult and relatively low juvenile survival. In this respect, point estimates of Mexican spotted owl survival probabilities appear similar to those of both northern (Burnham et al. 1996, Anthony et al. 2006) and California (Franklin et al. 2004, LaHaye et al. 2004) spotted owls. However, it is important to note that the temporal variability of survival rates of Mexican spotted owls appears greater than that of the other subspecies (Gutiérrez et al. 2003).

E. Environmental Variation and Vital Rates

Conservation and recovery of wildlife populations requires information about the factors that influence rates of population growth. This entails knowledge of environmental and human-induced agents that influence the owl’s reproduction, survival, and ultimately abundance over time. Several studies on northern and California spotted owl populations have examined sources of variation in associated vital rates (i.e., survival and reproduction; Franklin et al. 2000, 2004, Olson et al. 2004, Blakesley et al. 2005, Dugger et al. 2005, Anthony et al. 2006, Glenn et al. 2011). However, only one study of two Mexican spotted owl populations has been conducted long enough (11 years) to examine rigorously sources of variation in both survival and reproduction (see Seamans et al. 2002, Gutiérrez et al. 2003). Another study (Ward 2001) was only able to examine influences of environmental variation on reproductive rates, and this study
also was of shorter duration (six years). Here we briefly summarize some pertinent patterns in variation of vital rates, then discuss some specific environmental factors that may cause change in survival and reproduction of Mexican spotted owls.

a. **Types of Variation in Vital Rates.**—Spotted owls show considerable temporal and spatial variation in vital rates (Franklin et al. 2000, 2004, Ward 2001, Gutiérrez et al. 2003, Anthony et al. 2006, Glenn et al. 2011). Franklin et al. (2000) found that climate explained all of the temporal process variation (variation due to ecological processes rather than variation due to sampling) in vital rates of a northern spotted owl population, and habitat conditions explained most of the spatial process variation. This is intuitively logical: forest habitat conditions vary considerably over space but little over short time intervals such as annual breeding cycles of owls. Thus, we would expect habitat conditions to be linked to spatial variability in survival and fecundity, but not to short-term fluctuations in these vital rates. We also should expect that the magnitude of effects from various sources on spotted owl vital rates will differ among regions because environmental factors that can influence those rates also will vary (for example, see Ward and Block 1995, LaHaye et al. 2004).

Temporal and spatial variation in vital rates of two Mexican spotted owl populations studied by Gutiérrez et al. (2003) was roughly 2 to 5 times greater than in the population studied by Franklin et al. (2000). In addition, Gutiérrez et al. (2003) found that temporal variability in fecundity was far greater than temporal variability in survival for these populations.

b. **Effects of Weather on Vital Rates.**—Both survival and reproduction of Mexican spotted owls can be influenced by weather. However, with the exception of the direct influence of overheating or chilling of young, most effects will be manifested through the interaction between energetic demands and food supply. Both thermoregulation and prey availability can be influenced by physical environmental variables determined by regional climate, such as temperature and precipitation.

Seamans et al. (2002) modeled the influence of climate-related factors on temporal variation in vital rates, and Gutiérrez et al. (2003) expanded this effort to include models of spatial variation. Both vital rates appeared to be influenced by precipitation, but the nature of the relationship varied between study areas. In Arizona, a moisture index (the Palmer Z index) explained much of the temporal variation in both owl survival and fecundity. In New Mexico, the best approximating model included rainfall from the previous monsoon season (Jul – Sep) but explained little of the temporal process variation in fecundity and none of the variation in survival. Survival varied more spatially than temporally in these populations (Gutiérrez et al. 2003). The examined habitat covariates explained little of the spatial variation in owl vital rates for either study area.

Ward (2001) examined factors that might influence reproductive potential (number of young produced in a territory relative to the maximum number of young that could be produced) of Mexican spotted owls in southern New Mexico. Several *a priori* models were developed and compared. These models included different combinations of covariates describing climate, cover type, and available prey biomass over a six-year period. He found that: 1) models including factors describing climate or prey availability were better predictors of owl reproductive
potential than models that included only habitat variables; 2) models that included factors related to both weather and prey availability were better predictors than models that included only weather or prey availability; and, 3) models that included availability of prey aggregated among species were better predictors than models that included availability of single prey species. However, these models explained relatively little of the observed variation in owl reproductive potential and the strongest correlation observed was between a different measure of reproduction (reproductive output) and available biomass of mice and voles \((r = 0.77, P = 0.07, n = 6\) yrs).

Lavier (2006) studied the influence of temporal variation on aspects of site occupancy by Mexican spotted owls in the Sacramento Mountains, New Mexico. Winter precipitation was negatively correlated with site extirpation, whereas spring precipitation was positively correlated. Both monsoon and winter precipitation were positively correlated with site colonization, while spring precipitation was negatively correlated with colonization. Lavier (2006) suggested that spring, winter, and monsoon precipitation may influence probabilities of site extirpation or colonization through their effects on Mexican spotted owl survival and reproduction, respectively, and concluded that variability in weather had a greater influence on site occupancy than spatially related habitat effects (see next section). As noted earlier (see Diet and Prey Selection, above), weather also appeared to influence owl territory occupancy and productivity in the canyonlands of southern Utah indirectly by influencing prey abundance and diversity (Willey and Willey 2010).

c. Effects of Habitat on Vital Rates.— Expanding on their study of temporal variation and Mexican spotted owl vital rates, Gutiérrez et al. (2003) included models of spatial variation in habitat. They found that survival varied more spatially than temporally in two populations studied (one in northern Arizona and the other in west-central New Mexico), but the habitat covariates examined explained little of the spatial variation in owl vital rates for either study area.

Lavier (2006) evaluated amounts and spatial patterns of forested patches in areas occupied by Mexican spotted owls in the Sacramento Mountains, New Mexico. Few spatially explicit habitat variables were significantly correlated with rates of site extirpation or colonization or the probability of site occupancy. Amounts and spatial arrangement of landscape habitat features showed no apparent influence on site extirpation probabilities, but amount of interior forest and the density of interior forest patches within a site had a positive effect on site colonization, and amount of meadow habitat had a negative effect. In general, habitat variables appeared to influence site occupancy less than weather variables (see preceding section).

d. Effects of Prey on Vital Rates.— Several studies have shown that successfully breeding northern and California spotted owls consume more large prey (e.g., woodrats) than pairs that do not breed successfully (Barrows 1987, Laymon 1988, Thrailkill and Bias 1989, White 1996, Smith et al. 1999). However, this relationship did not hold in all studies of northern spotted owls, even in areas where this owl is known to select for larger prey like dusky-footed woodrats (Ward et al. 1998, Forsman et al. 2001). Similarly, successfully breeding Mexican spotted owls in northern Arizona and west-central New Mexico did not consume larger prey than non-breeding pairs (Seamans and Gutiérrez 1999). These inconsistent results may reflect the fact that diets are quantified from pellets gathered opportunistically, which may not adequately represent
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). Most predators are opportunistic and will shift to taking alternative prey when preferred prey species are not as available. In Ward’s (2001) study in the Sacramento Mountains of southern New Mexico, Mexican spotted owls appeared to prefer Mexican woodrats, but the amount of woodrats consumed was not correlated with owl reproduction. Rather, owl reproductive output across six years of study was correlated with the combined biomass of two species of Peromyscid mice and two species of voles in approximated home ranges of the owl. Ward (2001) suggested that woodrats may be selected for by Mexican spotted owls because they provide a consistent staple for survival, and individual owls must survive before they can reproduce. Reproduction in this population, however, occurred when mice and voles were more abundant. Thus, in this landscape, overall prey biomass exerted more influence on the owls’ reproduction than did the abundance of any single prey species. Seamans and Gutiérrez (1999) reached a similar conclusion for Mexican spotted owls, and Rosenberg et al. (2003) cautioned that simple prey-relationship models were unlikely to account for the highly synchronous temporal patterns observed in reproduction by northern spotted owls.

When comparing multiple spotted owl populations across the species range, Ward (2001) also demonstrated that the proportion of woodrat biomass in the diet was inversely related to temporal variation in reproductive output by spotted owls. Mexican spotted owls in the Sacramento Mountains, New Mexico, consumed the lowest proportion of woodrat biomass and showed the highest variation in young produced over time (Ward 2001: Fig. 4.7). Two other populations of Mexican spotted owls, one in northern Arizona and one in west-central New Mexico (Seamans et al. 1999), consumed moderate amounts of woodrat biomass. These populations showed less variation in reproductive output than the population in the Sacramento Mountains, but higher variation than recorded for northern spotted owls dwelling in northwestern California (Franklin et al. 2000). Based on these results, Ward (2001) suggested that management aimed at increasing woodrat abundance might reduce temporal variation in owl reproduction.

As noted earlier (see Diet and Prey Selection), prey abundance and diversity, as mediated by precipitation, also appeared to influence owl territory occupancy and productivity in the canyonlands of southern Utah indirectly, presumably by influencing food availability (Willey and Willey 2010).

Despite concerted efforts to understand the influence of environmental variation on owl vital rates, considerable uncertainty remains. Limited or inconsistent evidence indicates that temporal variation in owl vital rates is influenced directly by climate, especially precipitation, and by prey availability. Because estimated vital rates appeared responsive to precipitation several months prior to the estimation period, Gutiérrez et al. (2003) speculated that precipitation influences vital rates through an indirect mechanism that might involve precipitation influencing primary productivity, prey population dynamics, and ultimately owl vital rates, and work in southern Utah appeared to support this hypothesis (Willey and Willey 2010). However, when examined over the short-term and in a different study area and owl population (Ward 2001), these
pathways were not supported by empirical data. That is, each of several common prey species showed different associations with precipitation, temperature, and abundance of different plant species, and they demonstrated asynchronous population dynamics. Key interactions among climate, microhabitat condition, and food will influence energy and water balance of individual members of spotted owl populations but these more complex interactions have not been quantified due to lack of long-term or experimental study. We still have much to learn about how these more complex interactions are related to vital rates of Mexican spotted owls.

F. Fatality Factors

Several fatality factors (discussed below) have been identified as potentially important with respect to the Mexican spotted owl. Remains of a number of radio-marked owls have been found following death and examined by both field biologists and laboratory personnel, but most owls simply disappear. Further, cause of death often is difficult to impossible to determine even for owls that are found. Consequently, we know little about the extent or relative importance of factors that cause fatality.

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

Some of the factors discussed below can influence owl populations by impacting reproduction in Mexican spotted owls as well as by causing fatality directly. To reproduce, individuals must not only survive to a breeding period, but also 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 for reproduction.

a. Predation.—Predation may be a common fatality factor of Mexican spotted owls, accounting for at least five of 11 deaths documented among radio-marked adult and subadult Mexican spotted owls (Table B.7), and 14 of 29 documented fatalities of radio-marked juveniles (Ganey et al. 1998: Table 1 and Willey and van Riper 2000: Table 1). Predation may account for more deaths than recorded, because cause of death is often unknown. The specific predator is typically unknown. Procyonid mammals were observed attempting to raid cliff nests occupied by Mexican spotted owls in southern Arizona (Russell Duncan, Southwestern Field Biologists, pers. comm.), suggesting that they may prey on Mexican spotted owls. However, avian predation is suspected to be the main form of predation. Potential avian predators of Mexican spotted owls include great horned owls, northern goshawks (Accipiter gentilis), red-tailed hawks (Buteo jamaicensis), golden eagles (Aquila chrysaetos), and barred owls (where they are sympatric; Leskiw and Gutiérrez 1998). Some of these predators occupy the same general habitats as the Mexican spotted owl, but there is little direct evidence that they prey on Mexican spotted owls (Gutiérrez et al. 1995). Ganey (1988) reported one instance of apparent great horned owl predation on an adult Mexican spotted owl, and Richard Reynolds (RMRS, pers.
comm.) observed a golden eagle preying on a Mexican spotted owl. Results from radio-marked Mexican spotted owls indicate that all age classes are preyed upon (Ganey 1988, Ganey et al. 1998, 2005, Willey 1998a, Willey and van Riper 2000).

b. **Starvation.**—Starvation has not been observed in many deaths of adult and subadult owls (Table B.7), and generally occurred in mid-winter (J. L. Ganey, RMRS, unpubl. data). In contrast, starvation apparently accounted for 15 of 29 documented deaths of radio-marked juveniles, and occurred throughout the dispersal period (Ganey et al. 1998:Table 1; Willey and van Riper 2000:Table 1). Juvenile spotted owls may be more vulnerable to starvation than adults because of their poor hunting skills (Gutiérrez et al. 1985, Miller 1989, Ganey et al. 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 et al. 2005: Fig. 1). In addition, starvation may predispose young or even adults to predation (see Ganey et al. 2005). When starvation occurs in resident adults due to low prey populations that are regionally synchronous, this form of fatality can influence a number of owls at one time. When low survival is combined with lack of reproduction, population decrease can be rapid. There is evidence that this occurs in some Mexican spotted owl populations (Seamans et al. 1999, Ward 2001).

### Table B.7. Kaplan-Meier estimates of annual survival of adult or subadult radio-marked Mexican spotted owls in different study areas.

<table>
<thead>
<tr>
<th>Study area(s)2</th>
<th>Owls</th>
<th>Owl-years3</th>
<th>Annual survival</th>
<th>Fatality factors1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>SFP, WM, WC</td>
<td>8</td>
<td>12</td>
<td>0.88</td>
<td>0.12</td>
</tr>
<tr>
<td>Bar-M</td>
<td>13</td>
<td>26</td>
<td>0.79</td>
<td>0.10</td>
</tr>
<tr>
<td>SM-mesic</td>
<td>6</td>
<td>20</td>
<td>0.87</td>
<td>0.09</td>
</tr>
<tr>
<td>SM-xeric</td>
<td>7</td>
<td>13</td>
<td>0.62</td>
<td>0.14</td>
</tr>
</tbody>
</table>

1 P = suspected predation, S = starvation, U = unknown cause of death.

2 Study areas: SFP = San Francisco Peaks; WM = White Mountains; WC = Walnut Canyon (all in Arizona, UGM EMU, see Ganey [1988]); Bar-M = Bar-M Canyon, Arizona (UGM EMU, see Ganey et al. 1999); SM-mesic and SM-xeric refers to mesic and xeric study areas within the Sacramento Mountains, New Mexico, respectively (BRE EMU, see Ganey et al. [2005]). Bar-M Canyon area was dominated by ponderosa pine-Gambel oak forest. The Sacramento Mountains – xeric study area also was dominated by dry forest types, whereas all other study areas (SFP, WM, SM-mesic, WC) either were dominated by or contained significant amounts of mixed-conifer forest.

3 Number of owl years = (number of owls radio-marked x number of years marked owls were monitored). This figure is approximate.
c. **Accidents.**—Accidents may be another fatality factor. For example, in some portions of their range, Mexican spotted owls have been viewed perched on the ground or on fence posts adjacent to roads (J. P. Ward, FWS, pers. comm.) and there are documented cases of Mexican spotted owls being hit by cars (Roger Skaggs, Glenwood, New Mexico, pers. comm.; Russell Duncan, Southwestern Field Biologists, pers. comm.; J. L Ganey, RMRS, unpubl. data; S. Hedwall, FWS, unpubl. data). The type of roads at which fatalities 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.

d. **Disease and Parasites.**—Little is known about how disease and parasites affect spotted owls. A northern spotted owl found dead was diagnosed with an infection by a relapsing fever-like *Borrelia* species (Thomas et al. 2002). The mechanism of exposure was unknown. The principal vectors known to transmit similar diseases are soft-bodied ticks, making transmission by nest-dwelling parasites a possibility. However, direct transmission from prey may be more likely, as small rodents, which constitute the primary food of spotted owls, serve as reservoirs for relapsing fevers (Thomas et al. 2002). Until more is known about the means of transmission, the potential importance of this disease with respect to spotted owls is unknown.

One disease of particular concern to birds in general is West Nile virus (WNV). This virus was first isolated in Africa and first appeared in the U.S. in 1999, in New York (see reviews in Blakesley et al. 2004, McLean 2006). It spread rapidly across the country and has now reached the range of the Mexican spotted owl. The virus is commonly spread by transmission between mosquito vectors and bird reservoir hosts. However, birds can also become infected by means other than arthropod transmission (Marra et al. 2004). Komar et al. (2003) reported that ingestion of WNV in aqueous solution resulted in infection in several bird species, including great horned owls. It is not known whether ingestion of infected prey by raptors has resulted in bird fatality, but the risk exists (Marra et al. 2004). Finally, contact transmission has been documented in the laboratory in caged birds (McLean et al. 2001; Komar et al. 2003), perhaps from such behaviors as mutual preening and beak-to-beak contact.

Avian fatality from WNV has been extensive in North America (Komar et al. 2003). Natural fatal infections were detected between 1999 and 2002 in over 28,000 bird carcasses representing 198 species, including a captive spotted owl (subspecies not identified; Center for Disease Control unpubl. data). However, we are unaware of any records of wild spotted owls being infected with WNV. Hull et al. (2010) tested 209 California spotted owls in the Sierra Nevada of California between 2004 and 2007 and detected no antibodies in those specimens, despite numerous recorded infection incidences in other avian species in the region during that time. Hull et al. (2010) concluded that WNV infection likely was absent in the area’s spotted owls, but they also noted that an absence of detections could indicate that spotted owls exposed to WNV do not survive long enough to develop a detectable immune response.
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. Nonetheless, the potential impact of the disease on threatened species and those of ecological importance is of great concern (Joyner et al. 2004). The scientific panel that reviewed the status of and threats to the northern spotted owl was unanimous in regarding WNV as a potential future threat (Blakesley et al. 2004).

Thus, the impact of WNV on Mexican spotted owls is difficult to predict. In general, we know little about the abundance and behavior of the relevant vectors in areas occupied by Mexican spotted owls, making it difficult to predict infection rates. We also do not know how many of the owls infected by WNV will die or suffer reduced viability, or whether or not owls will develop some level of immunity to the disease following initial exposure. Thus, all we can say with certainty at this time is that WNV has arrived and has the potential to significantly impact population viability of Mexican spotted owls.

Relative to parasites, Young et al. (1993) found Hippoboscid flies on 17% of 382 live northern spotted owls examined for parasites, and Hunter et al. (1994) found Hippoboscid fly larvae in the ears of six of 18 live Mexican spotted owls examined. Hunter et al. (1994) also found a larval mite and lice on two of 28 museum specimens of Mexican spotted owls examined, and some of the live owls examined also had lice. Neither study reached firm conclusions concerning fatality and ectoparasites in spotted owls, but Hunter et al. (1994) 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. Further, Young et al. (1993) noted that hippoboscid flies are vectors for several hematotoan (blood-borne) parasites in birds.

Infection rates of such blood-borne parasites appear to be high in spotted owls. For example, Gutiérrez (1989) found an infection rate of 100 percent in a survey of blood parasites in all three subspecies of spotted owls. More recently, a survey in northern and California spotted owls found infection rates of 52 and 79% respectively (Ishak et al. 2008). Infection rates of spotted owls were far greater than rates in sympatric barred owls (15%), and spotted owls were far more likely than barred owls to harbor multi-species infections (Ishak et al. 2008). These high infection rates and the numbers of spotted owls with multiple infections support the hypothesis that spotted owls have weaker immune systems than sympatric barred owls, and this may provide barred owls with a competitive advantage (Ishak et al. 2008).

The effects of both parasites and disease likely vary depending on the condition of individual owls. Thus, infections that are normally nonpathogenic can assume greater importance in owls that are stressed or malnourished (Young et al. 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. Similarly, as noted above, disease and parasite infections could influence the outcome of, for example, interactions with competitors.
G. Other Ecological Interactions

a. Interspecific Competition.—Several other species of raptors and owls occur within the range of the Mexican spotted owl. Raptors may compete with Mexican spotted owls for resources such as nest sites, but tend to 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.

In general, we know little about potential competitive relationships among sympatric owl species within the range of the Mexican spotted owl. Logically, the two species most likely to compete directly with Mexican spotted owls are the great horned owl and the barred owl, based on their relative size, natural history, and, in the case of the barred owl, genetic similarity. Throughout much of the range of the Mexican spotted owl, the most likely competitor is the great horned owl (USDI FWS 1995). This owl is larger than the Mexican spotted owl, is sympatric with Mexican spotted owls throughout their range, and both owls are active at night, suggesting that they could compete for nocturnally active prey (Gutiérrez et al. 1995, Houston et al. 1998). The great horned owl and the barred owl may prey on spotted owls (Forsman et al. 1984, Ganey 1988:185, Gutiérrez et al. 1995), and spotted owls in turn may prey on other smaller owls (e.g., Ganey 1988: Table 20).

Despite this potential for competition and possible predation by great horned owls on Mexican spotted owls, little is known about interspecific interactions between the two. Some evidence suggests that Mexican spotted owls may avoid areas occupied by great horned owls (e.g., interference competition). For example, Phillips et al. (1964) reported that great horned owls colonized an area previously occupied by Mexican spotted owls following a fire that opened up the forest canopy. Spotted owls were not heard in this area in subsequent years. Similarly, Johnson and Johnson (1985) reported that once great horned owls moved into areas previously occupied by Mexican spotted owls, they seldom heard Mexican spotted owls in those areas.

In contrast, Ganey et al. (1997) reported considerable spatial overlap among home ranges of sympatric, radio-marked spotted and great horned owls in Arizona. On average, Mexican spotted owls shared 51.0 ± 24.3% (SE) of their breeding-season home range and 74.1 ± 4.8% of their non-breeding-season home range with great horned owls (n = 6 Mexican spotted owl and 3 great horned owl home ranges). The figures for proportions of great horned owl home ranges shared with Mexican spotted owls were similar (57.4 ± 12.2 and 70.5 ± 12.3% for breeding- and non-breeding-season home ranges, respectively; Ganey et al. 1997: Table 2). Both species of owls sometimes foraged in the same forest stands. These stands were not necessarily used at the same time, however, and Mexican spotted owls also foraged in many stands that great horned owls did not appear to forage in (Ganey et al. 1997: Table 3). Home-range composition, in terms of cover types and canopy-cover classes, did not differ between species in either the breeding or non-breeding season (Ganey et al. 1997: Table 4). In contrast, use of cover types and canopy-cover classes within the home range differed between species in at least some combinations of season and activity considered (Ganey et al. 1997: Table 4). Differences were typically greatest with respect to roosting habitat used during the breeding season. For example, >90% of roosting locations for Mexican 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% (Ganey et al. 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 Mexican spotted owl foraging locations occurred in forests with canopy cover >40% during both seasons. Spotted owls roosted primarily in pine-oak forest during both seasons, sometimes roosted in ponderosa pine forest, and did not roost in meadow cover types (Ganey et al. 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. Stands used by foraging Mexican spotted owls contained greater volumes of logs and greater shrub cover than stands used by great horned owls during both seasons. During the non-breeding season, stands used by foraging Mexican spotted owls also had greater canopy cover, whereas stands used by great horned owls had greater forb cover (Ganey et al. 1997). These observations are consistent with the hypothesis that Mexican 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 (Buchanan et al. 2004, Hamer et al. 2007).

Avoidance of competition by partitioning food was less apparent. Diet overlap was considerable between Mexican spotted and great horned owls in the same study area where habitat partitioning was observed (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 = 1125 and 94 prey items for Mexican spotted owls and 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 Mexican spotted owls and 47.0 ± 7.4 g for great horned owls when all prey were included. For all non-insect prey (n = 746 and 63 items for spotted and great horned owls, respectively), mean prey mass was 60.0 ± 2.4 g for Mexican spotted owls and 69.7 ± 9.8 g for great horned owls. 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 (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. These results suggest a potential for both exploitation and interference competition for food resources, which are assumed to be limiting in some years (Verner et al. 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 Mexican spotted owls primarily using forests with canopy cover >40%, and great horned owls primarily using forests with canopy cover <40%. 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 et al. 1995, Houston et al. 1998), as well as with morphological and
behavioral characteristics of both species (Ganey et al. 1997). This seems to suggest that habitat use was not strongly influenced by the presence of the potential competitor. We observed numerous instances of apparently agonistic calling encounters between radio-marked owls, however (J. L. Ganey, RMRS, pers. obs.; see also Ganey 1990). This suggests the possibility 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 likely take similar prey in different areas, minimizing direct competition for resources. This interaction could be altered if extensive forest management occurs and reduces the area of forests with canopy cover >40%. This change could benefit the great horned owl and reduce habitat quality for the Mexican spotted owl (Ganey et al. 1997).

We also know little about possible competitive interactions between barred owls and Mexican spotted owls. The barred owl is considered a significant threat to northern spotted owls, however (Kelly et al. 2003, Gutiérrez et al. 2004, 2007, Kelly and Forsman 2004, Levy 2004, Olson et al. 2005, Buchanan et al. 2007, Kroll et al. 2010). Overlap between northern spotted owls and barred owls appears to be high in both habitat use (Herter and Hicks 2000, Kelly et al. 2003, Pearson and Livezey 2003, Buchanan et al. 2004, Olson et al. 2005, Hamer et al. 2007, Bailey et al. 2009, Singleton et al. 2010) and diet (Hamer et al. 2001). In addition, these owls are known to hybridize (Hamer et al. 1994, Haig et al. 2004b, Kelly and Forsman 2004, Seamans et al. 2004), suggesting that competition for mates also occurs. In many areas, numbers of barred owls are increasing, whereas numbers of spotted owls are decreasing, suggesting that the larger and more aggressive barred owls are competitively dominant and are displacing spotted owls (Kelly et al. 2003, Gutiérrez et al. 2004, 2007, Kroll et al. 2010; but see also Crozier et al. 2006, Livezey and Fleming 2007, Van Lanen et al. 2011). A recent study also suggested that barred owls may gain a competitive advantage over sympatric spotted owls due to lower infection rates with blood-borne parasites (Ishak et al. 2008; see Diseases and Parasites, above). Records of possible predation of spotted owls by barred owls also exist (Leskiw and Gutiérrez 1998).

The barred owl may be sympatric with Mexican spotted owls in Mexico (Williams and Skaggs 1993, Howell and Webb 1995, Holt et al. 1999), but little is known about patterns of either distribution or habitat use of either owl in the apparent zone of sympatry (Williams and Skaggs 1993, Enriquez-Rocha et al. 1993). Thus, there may be potential for interspecific competition to occur in Mexico, but the extent of such competition (if any) is unknown.

Barred owls historically have not co-occurred with Mexican spotted owls within the U.S., with the possible exception of southern Texas. Both species have been reported occasionally from the vicinity of Big Bend National Park (Wauer 1996). We do not know if either or both species are regular residents in that area, however. There also are recent confirmed records of barred owls in northern and eastern New Mexico (Williams 2005, cited in Cartron 2010, H. Walker, NMGFD, pers. comm.). Whether such records indicate a range expansion by barred owls or simply vagrant individuals is unknown. Thus, there does not appear to be much opportunity for competition between barred and Mexican spotted owls in the U.S. at present, but that could change if the barred owl expands into the range of the Mexican spotted owl.
In summary, we know relatively little about competitive relationships between Mexican spotted owls and other owls. Competition for food resources also may extend to medium-sized and small carnivores that consume large amounts of nocturnal rodents and that hunt in habitats similar to Mexican spotted owls. This would include species like bobcat (*Lynx rufus*), gray-fox (*Urocyon cinereoargenteus*), ring-tailed cat (*Bassariscus astutus*), and coyote (*Canis latrans*). Better information clearly is needed to assess the potential occurrence and importance of such competition, as well as to understand the potential influence that forest management might have on competitive interactions.

### b. Human Disturbance

Although a variety of human-caused disturbances can affect birds of prey and other wildlife (Knight and Gutzwiller 1995), we know relatively little about the effects of human disturbance on Mexican spotted owls. Delaney et al. (1999b) and Johnson and Reynolds (2002) studied the response of Mexican spotted owls to overflights by helicopters and fixed-wing aircraft, respectively. Both studies suggested that owls were fairly resilient to short-duration disturbance caused by overflights. Delaney et al. (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 chainsaws. Mexican spotted owls were more sensitive to disturbance by chainsaws than by helicopter overflights at comparable distances, and chainsaw operation caused most owls to flush from their perches when chainsaws were operated <60 m (197 ft) from roosting Mexican spotted owls. Owl response decreased with increasing distance to noise source for both chainsaw operation and helicopter overflights, and Delaney et al. (1999b) suggested that a buffer zone of 105 m (344 ft) would minimize impacts of helicopter overflights on Mexican 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 Mexican spotted owl habitat. They found consistent differences in noise levels among 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. Delaney and Grubb (2004) concluded that owls were capable of hearing all sound sources tested at distances of at least 400 m. Owl response to these noise sources was not evaluated in this study. In a study on northern spotted owls, however, Hayward et al. (2011) found that owls close to noisy roads fledged significantly fewer young than owls close to roads. They concluded that routine traffic exposure may decrease reproductive success of northern spotted owls over time.

Swarthout and Steidl (2001, 2003) experimentally evaluated the effects of hikers on Mexican spotted owls in canyonlands terrain. They quantified both flush responses and activity budgets of owls exposed to hikers. Owls exposed to hikers sometimes flushed 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 potentially could be detrimental to owls, but likely would be detrimental only where owls occupied canyons receiving use by ≥50 hikers per day. Swarthout and Steidl (2001) concluded that placing a 55-m (180-ft) buffer zone around known owl roosting
sites would eliminate most flush responses. However, a buffer of this size also would restrict hiker access to 80% of the narrow canyons occupied by Mexican spotted owls. They concluded that a less conservative 12-m (39-ft) 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. Further, at least one study of northern spotted owls documented a significant effect of increased road noise on reproductive success, suggesting that human disturbance may impact fitness parameters of spotted owls.

H. Climate Change

In addition to changes in distribution and amounts of the owl’s habitat, climate change may result in direct and indirect influences on the owl’s population demography and interactions with other species. Much of the evidence for these potential influences was presented in the preceding sections that detailed the owl’s population ecology, but we summarize some additional examples here.

a. Changes in Demographic Rates.—Shifts in key weather variables may influence owl demography by influencing the physiology of individual owls. For example, if climate change results in more or longer periods where microclimatic temperatures exceed lower or upper critical limits, owls will require additional energy and/or water to maintain homeostasis (Ganey et al. 1993, Weathers et al. 2001). If owls are not able to adopt new behaviors to counter these additional energetic demands, such as finding roost sites with greater thermal protection, they will have less energy to allocate to reproduction and/or survival. Should temperatures increase enough that all available microclimates exceed the owl’s lethal limits, the owls must disperse elsewhere to inhabitable environments. Because climate change will likely create shifts in weather over large areas and because long-distance dispersal (>150 km [93 mi]) is not very plausible for most Mexican spotted owls, shifts in temperatures that regularly exceed critical or lethal limits will result in greater fatality and declining populations. Changes in water balance may be as important as changes in energy balance (see Weathers et al. 2001), particularly if climates become both warmer and more arid.

Annual weather patterns are associated with survival and reproduction of spotted owls (Franklin et al. 2000, 2004, North et al. 2000, LaHaye et al. 2004, Olson et al. 2004, Dugger et al. 2005, Anthony et al. 2006, Seamans and Gutiérrez 2007). Precipitation may influence the owl’s reproductive output either directly or indirectly. Direct negative effects of increased precipitation during the nesting period on survival and especially reproduction have been shown in other subspecies of spotted owls (e.g., Franklin et al. 2000, North et al. 2000, LaHaye et al. 2004). This direct negative effect has not been documented in Mexican spotted owls, however.

In a study on two populations of Mexican spotted owls, Seamans et al. (2002) documented positive relationships between precipitation (i.e., precipitation during the previous year, during the previous winter, or during the previous monsoon season) and survival and reproductive
Seamans et al. (2002) speculated that precipitation was probably important in providing indirect benefits to Mexican spotted owls. Specifically, they hypothesized that germination and sprouting of annual plants during the monsoon season may extend the breeding season of small mammals in the Southwest and may increase overwinter survival and therefore abundance of prey. Many prey species eaten by Mexican spotted owls exhibit high temporal variability in abundance (Ward and Block 1995, Ward 2001, Block et al. 2005), and owl reproduction appears linked to changes in prey biomass (e.g., Ward and Block 1995, Ward 2001). Thus, changes in climate that affect prey abundance likely also will affect owl reproduction. Interactions among temperature and moisture regimes may differ across elevational gradients in the Southwest, thus affecting small mammal populations differently in different areas (Seamans et al. 2002:331). Climate changes that decrease prey availability may also negatively influence the owl’s water balance, especially when non-metabolic water is not available.

In the only direct study on the effects of climate change on demographic rates of Mexican spotted owls, Peery et al. (2011) used the demographic data from the study areas discussed in Seamans et al. (2002, see above) to evaluate how climate change might influence population dynamics and extirpation risk of Mexican spotted owls. They used stochastic, stage-based matrix models, parameterized with vital rates linked to annual climatic variation, to project owl populations forward in time under both current climatic conditions and three IPCC emissions scenarios (B1, A1B, and A2; IPCC 2007). Resulting models showed that populations in both the Arizona and New Mexico study areas declined rapidly over the next century under all three emissions scenarios, and extirpation risk for both populations was much higher under all three scenarios than under current climatic conditions. Results were driven largely by negative effects of warm, dry conditions on Mexican spotted owl fecundity and survival, with those effects far greater for fecundity than for survival. Changes in population growth rates were more sensitive to predicted increases in temperature than to predicted declines in precipitation. Peery et al. (2011) concluded that Mexican spotted owls were highly vulnerable to climate change even in core portions of their range.

Peery et al. (2011) also evaluated the effects of climate change on a population of California spotted owls from the San Bernardino Mountains, California. Again, they used existing demographic data (LaHaye et al. 1994, 2004) and the same three IPCC scenarios, and projected the California spotted owl population forward in time. Unlike the Mexican spotted owl populations analyzed, the California spotted owl population was relatively insensitive to predicted changes in climate, and extirpation risk for this population was low under all climate scenarios modeled. This difference was due primarily to a negative relationship between fecundity of California spotted owls and cold, wet springs, and the fact that such springs were less common under predicted climate scenarios. This suggests that responses of populations of spotted owls to climate change may differ among geographic regions. Whether such variation will occur within the range of the Mexican spotted owl remains unknown, however.

The study by Peery et al. (2011) necessarily relied on models rather than observed population responses to climate change. Nevertheless, they used a rigorous modeling framework, the best available demographic data, and relationships between that demographic data and annual variation in climate derived from sound empirical studies to parameterize models. Consequently,
we view their results as robust and sobering, especially because the models evaluated by Peery et al. did not include potential changes in disturbance regimes caused by climate changes.

b. Reduction in Population Size.— At this time, no empirical evidence exists documenting changes in Mexican spotted owl distribution or population size due to climate change. As mentioned above, however, both survival and reproduction were positively correlated with precipitation in two populations studied (Seamans et al. 2002), and a simulation study conducted by Peery et al. (2011), suggested that increasingly warmer and drier climates would greatly increase extirpation risk for Mexican spotted owls in study areas in Arizona and New Mexico.

c. Changes in Co-evolved Interactions.— Changing climates also could influence distribution patterns and abundance of major prey species, as well as potential competitors with and predators on Mexican spotted owls. Each species has different physical tolerances and resource requirements, including the small mammal species eaten by Mexican spotted owls (Ward 2001). This makes it hard to generalize about the effects of changing climates on prey distribution and availability. In examining the influence of habitat and weather-related covariates on the biomass (g ha⁻¹) of five common prey species of Mexican spotted owls in the Sacramento Mountains, New Mexico, Ward (2001) identified a spectrum of effects for each species. Deer mice were influenced by weather related effects that changed with time, whereas Mexican woodrats were more influenced by habitat related effects. Untested predictions about the order of species decline or loss of the five studied prey species in the Sacramento Mountains given their current distributions and natural histories (reviewed by Ward [2001: Chapter 2]) would suggest that drier warmer microclimates would result in loss of vole species first, followed by loss or a reduction in numbers of woodrats, and finally a reduction in numbers of peromyscid mice. The magnitude of such potential changes in the distribution and abundance remain untested at this time, however.

In rocky-canyon habitat in southern Utah, Willey and Willey (2010) documented increases in abundance and species diversity of rodents during a period of increased precipitation. Territory occupancy and territory re-colonization rates of Mexican spotted owls also increased during the period of increased precipitation, presumably in response to increases in prey abundance (Willey and Willey 2010). The strong apparent response of small mammals to precipitation in this study may have been a function of the semi-arid climate of the region. For example, a review of variation in responses by deer mice to increased precipitation in varying environments demonstrated that the greatest response occurred in arid regions and the lowest response occurred in the wet coastal forests of the Pacific Northwest (Ward 2001: Chapter 2).

d. Interactions With Competitors and Predators.— Changes in forest composition also could influence abundance and distribution of owl competitors and predators, but the magnitude and direction of such potential changes again are unknown at this time. Northern spotted owls are being affected by a direct competitor, the barred owl, which recently expanded its range into the Pacific Northwest and California (Gutiérrez et al. 2007). This species occurs in the eastern U.S. and portions of Mexico (Mazur and James 2000). Whether climate change will ultimately result in a sympatric distribution of Mexican spotted and barred owls is unknown. It is possible that warmer, drier conditions might favor such potential predators as great-horned owls (see
Predation, above), which occur in habitats ranging from high-elevation and high-latitude forests to hot deserts (Johnsgard 1988).

7. Movements and Migration

The ability of Mexican spotted owls to move within and among habitats or across a landscape is a key factor for assessing function and viability of populations over time. For example, small populations often require recruitment from larger (core) populations to persist for long periods. 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 Mexican spotted owls is often difficult to obtain, however, and details about conditions that allow for successful dispersal or explanations for periodic migrations are limited. Nonetheless, a few studies have documented movements of this owl. This section summarizes existing knowledge about movement patterns of the owl and the processes that influence its movements.

A. Seasonal Migration

Ganey and Block (2005a) summarized available information on seasonal movements and range use of radio-marked Mexican spotted owls, supplemented by anecdotal observations of owls during the non-breeding season, and evaluated the adequacy of management guidelines in protecting habitats used by owls during the non-breeding season. They operationally defined all radio-marked owls that moved >2 km (1.2 mi) 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 (see Space Use above).

Seasonal movements or migration occurred in most areas where movements of radio-marked owls were monitored (Table B.8). Seasonal migration generally involved a subset of the population, with the size of that subset varying both among study areas and years (Table B.8). Migrating owls typically left study areas in November or December, and returned from January to April (Table B.9). Distance moved ranged from 5 to 50 km (3 to 31 mi) 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 kilometers, suggesting that some owls may move long distances (see also Gutiérrez et al. 1996).

Duncan and Speich (1995) provided additional evidence for down-slope migration in Mexican spotted owls. They documented a subadult owl overwintering in Sonoran riparian deciduous woodland (Brown et al. 1980) at 838 m in the foothills of the Santa Catalina Mountains, Arizona. They relocated this owl five years later as a member of a territorial pair near the summit of this range, at an elevation of 2,560 m (8,399 ft). 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, however, it is impossible to determine whether these represented migrating territorial owls or dispersing juveniles, which use similar habitats (Arsenault et al. 1997, Ganey et al. 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 (Table B.9). Partial migration also occurs in California spotted owls (Laymon 1989, Verner et al. 1992). In contrast, migration appears to be rare in northern spotted owls (Gutiérrez et al. 1995).

Reasons why only some owls migrate are unknown. In addition, some individual Mexican spotted owls migrate in some years, but not others (Table B.8). Migration generally entails a change in elevation for both Mexican (Table B.9) and California spotted owls (Laymon 1989, Verner et al. 1992), with most owls moving down slope (but see Willey 1998a). Migration to lower elevations allows owls to winter in areas that are warmer than their breeding areas during the winter 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 (Ward and Block 1995). 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 et al. 2005). For example, Block et al. (2005:625) used live trapping to estimate available winter prey biomass in both the traditional breeding area and a wintering area used by a pair of radio-marked Mexican spotted owls. They estimated that winter prey biomass was almost eight times greater within the wintering area than within the breeding area (1,200 g ha\(^{-1}\) vs. 155 g ha\(^{-1}\)). Although circumstantial, the evidence suggests that migration was driven by food availability.

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 (but see Peterson 2003). 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.

From a conservation perspective, some migrating owls occupy cover types that have no protected status under the original recovery plan for the Mexican spotted owl (USDI FWS 1995) or this revised Recovery Plan. These cover types also are used by dispersing juvenile owls during the fall and winter (Arsenault et al. 1997, Ganey et al. 1998, Willey and van Riper 2000). The types of lowland areas in which wintering owls have been observed cover vast areas, however, 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 Mexican spotted owls are necessary at this time, with the possible exception of portions of the foothills of the Front Range in Colorado. This region has experienced rapid growth and development since 1990.
Table B.8. Numbers of radio-marked Mexican spotted owls observed to migrate during the winter in various studies (from Ganey and Block [2005a]).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Years</th>
<th>Number of owls radio-marked</th>
<th>Number of owls migrating(^1)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Francisco Peaks</td>
<td>1986-1987</td>
<td>4</td>
<td>2</td>
<td>Ganey and Balda</td>
</tr>
<tr>
<td></td>
<td>(1989b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walnut Canyon</td>
<td>1986-1987</td>
<td>2</td>
<td>2</td>
<td>Ganey and Balda</td>
</tr>
<tr>
<td></td>
<td>(1989b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1990-1991</td>
<td>9</td>
<td>0</td>
<td>Zwank et al. (1994)</td>
</tr>
</tbody>
</table>

\(^1\) Migration was defined as movement >2 km (1.2 mi) from the center of the breeding-season home range.
Table B.9. Distance moved, movement duration, elevation change, and habitats used by migrating adult or subadult Mexican spotted owls (from Ganey and Block [2005a]).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Years</th>
<th>Sex</th>
<th>Distance moved (km)</th>
<th>Duration</th>
<th>Elevation change (m)</th>
<th>Cover type</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Francisco Peaks</td>
<td>1986-87</td>
<td>F</td>
<td>Unknown</td>
<td>Nov-Apr</td>
<td>Unknown</td>
<td>MC, PP, P/O/J, R</td>
<td>1</td>
</tr>
<tr>
<td>San Francisco Peaks</td>
<td>1986-87</td>
<td>M</td>
<td>Unknown</td>
<td>Nov-Apr</td>
<td>Unknown</td>
<td>MC, PP, P/O/J, R</td>
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</tr>
<tr>
<td>Walnut Canyon</td>
<td>1986-87</td>
<td>F</td>
<td>10</td>
<td>Dec-Jan</td>
<td>100</td>
<td>MC, PP, P/O/J, R</td>
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</tr>
<tr>
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<td>1986-87</td>
<td>M</td>
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<td>Dec-Jan</td>
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<td>PJW, SDS</td>
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1. Elevation changes are negative unless otherwise indicated.
2. Cover types: MC = mixed-conifer forest, MS = mountain shrub, PJW = pinyon-juniper woodland, PO = ponderosa pine-Gambel oak forest, PP = ponderosa pine forest, P/O/J = ponderosa pine/oak/juniper, R = riparian, SDS = semi-desert scrub, SF = Spruce-fir forest.
3. Sources: 1 = Ganey and Balda (1989b); 2 = Skaggs 1990; 3 = J. L. Ganey and W. M. Block (unpubl. data); 4 = Johnson (1997: Table 5); 5 = Willey (1998a:54-55).
4. Wintering areas not located despite an aerial search covering thousands of square kilometers.
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).
B. 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 (Gutiérrez et al. 1985). Breeding dispersal, or movement by subadult or adult individuals from a previously occupied territory to another, occurs less frequently (Gutiérrez et al. 1995, Forsman et al. 2002, Blakesley et al. 2006).

a. Natal Dispersal.— Dispersal by juvenile Mexican spotted owls has been studied directly by monitoring movements of radio-marked individuals in New Mexico (Arsenault et al. 1997), Arizona (Ganey et al. 1998), and Utah (Willey and van Riper 2000), and indirectly in Arizona and New Mexico by monitoring movements of color-banded juvenile owls (Duncan and Speich 2002, Gutiérrez et al. 2003).

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. In an effort to understand triggers of natal dispersal, Willey and Van Riper (2000) recorded observations of parent-offspring interactions and departure dates of juvenile Mexican that were supplemented with food and a control group without additional food. Juvenile owls that were provided with supplemental food all left their natal sites significantly sooner than juveniles that did not receive supplemental food. Aggressive behaviors among offspring and parents that might induce dispersal were not noticeably different between the two treatment groups, however. Thus, this study did not support the hypothesis that food shortage triggers natal dispersal in Mexican spotted owls. Rather, it suggested that body condition might positively influence departure. That is, acquiring sufficient energy reserves prior to embarking may be a key physiological factor in the timing of natal dispersal in spotted owls (Willey and van Riper 2000).

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 >92 km (<0.6 to >57.2 mi). These distances likely represent minimum estimates of dispersal capability, as only one of 62 radio-marked juveniles 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 from all studies used a wide variety of habitats, including some that were very different in structure and composition from typical breeding habitat. Because juvenile survival is typically low (<30% of these individuals apparently live to the next year), documenting final dispersal distances using radio-marked birds requires that a large number of young are radio-marked (>100) and followed for a longer (>3 years) period than most radio-transmitter batteries or funding for aerial monitoring will last (Forsman et al. 2002). However, the patterns observed for the smaller samples of Mexican spotted owls differed little from a more comprehensive study of natal dispersal of northern spotted owls in Oregon and Washington (Forsman et al. 2002). For example, natal distances observed in this long-term, large-sample study (n = 324 radio-marked and 711 banded juveniles followed from 1985—1996) ranged from 1.8 to 103.5 km (1.1 to 64.3 mi) for radio-marked
juveniles and from 0.6 to 111.2 km (0.4 to 69.1 mi) for re-sighted individuals originally color banded at natal sites. The distribution of these dispersal distances was skewed toward shorter distances with only 8.7% of the final distances between the natal territory and location of settlement being >50 km (31 mi). On average, male and female juveniles in this study eventually settled within an average of 4.2 and 7.0 territory widths from their natal sites after two to five years (Forsman et al. 2002).

Estimates of natal dispersal distances from mark-recapture studies also suggest that most California and northern spotted owls settle on territories within a few territory widths of their natal site (LaHaye et al. 2001, Forsman et al. 2002). These estimates may provide a better estimate of final distances traveled by successful dispersers than did the radio-telemetry studies discussed above, although the finite size of the mark-recapture study areas could underestimate this distance. For example, LaHaye et al. (2001) examined settling patterns of dispersing California spotted owls in the San Bernardino Mountains, California, within a 535-km² (132,201 ac) study area. They evaluated possible effects of study-area size on dispersal distances by nesting several successively smaller areas within their complete study area. They found that dispersal distances were underestimated when using band-resighting data for establishing settling patterns in the smaller nested study areas (see also Zimmerman et al. 2007). In contrast, Forsman et al. (2002) compared distance estimates based on radio-marked northern spotted owl juveniles with estimates derived from settling patterns and found no evidence that the small study areas used to study settling patterns biased distance estimates. Thus, it is unclear whether or not the finite size of demography study areas consistently results in underestimates of natal dispersal distances.

Unfortunately, few estimates of natal dispersal distance are available for the Mexican spotted owl. Duncan and Speich (2002) were able to document four instances of inter-mountain movement by dispersing Mexican spotted owl juveniles that had been marked with color bands at their birth sites. These movements required these owls to cross desert valleys between Sky Island mountain ranges in southeastern Arizona. Distances between natal sites and territories established by these four individuals ranged from 28 to 54 km (17 to 34 mi).

It is not clear when natal dispersal typically ceases in spotted owls. Gutiérrez et al. (2003) reported that 90 to 100% of fledged young that occupied territories in two demography study areas did so within three years. Patterns differed between their Arizona and New Mexico study areas, however. In Arizona, over 60% of fledged young that settled did so in their first year, with declining proportions of young settling through year five (Gutiérrez et al. 2003: Fig. 13a). In New Mexico, young settled in equal proportions in the first three years following fledging, with no recruitment observed in subsequent years (Gutiérrez et al. 2003: Fig. 13b). LaHaye et al. (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 et al. (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 two to five years old. Thus, available evidence 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.
b. 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 et al. 2001, Forsman et al. 2002, Gutiérrez et al. 2003, J. L. Ganey and J. P. Ward, unpubl. data).

Arsenault et al. (1997) noted apparent cases of dispersal in subadult Mexican spotted owls, and Gutiérrez et al. (1996) suggested that dispersal also may occur in adult Mexican spotted owls. In their more comprehensive study of northern spotted owls, Forsman et al. (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 0.01 to 85.2 km between previously and newly occupied breeding sites for all age classes. However, first-year subadults \( n = 71 \) moved farther than second-year subadults \( n = 75 \) and adults \( n = 294 \); median distances 5.1, 4.1, and 3.5 km [3.2, 2.5, 2.2 mi], respectively. Most (83%) adults that did disperse only moved once. Of those that moved twice or more, 41% moved backed to an original territory (Forsman et al. 2002). There were no significant differences in breeding dispersal distances among the sexes. The probability that an individual would move was generally greater for females, however, and was 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 disperse to another site on a much rarer and irregular basis. 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; see also Ganey and Block 2005a) or this revised Recovery Plan. There is little evidence from study of movements 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 one to two years 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, however, we know little about dispersal behavior, and especially about dispersal movements of Mexican spotted owls during and following their second summer of life.

8. Metapopulation Ecology

Many authors have noted that the structure and spatial distribution of spotted owls at a rangewide scale suggests that groupings of individuals may occur as subpopulations and that these subdivided populations may function as a metapopulation (e.g., 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 et al. 1992, LaHaye et al. 1994, Noon and McKelvey 1996.). Indeed, Gutiérrez and Harrison (1996) argued that spotted owl population dynamics and viability could be understood only in the context of a metapopulation. 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 unsuitable habitat.

Despite the important contributions made by metapopulation theory and models to management of northern and California spotted owls (Shaffer 1985, Noon et al. 1992, LaHaye et al. 1994, Gutiérrez and Harrison 1996, Noon and McKelvey 1996), few studies have examined metapopulation structure of Mexican spotted owls. Keitt et al. (1995, 1997) examined the spatial pattern of forest habitat patches across the range of the Mexican spotted owl. Their objective was to gauge the extent to which the owl might behave as a metapopulation in the classical sense of a set of local populations linked by infrequent dispersal. Such a finding, if verified, would suggest that population dynamics of owls in one local population might be influenced by factors, including management activities, which affected nearby populations. Conversely, if local populations are functionally discrete, then those populations could be treated separately with some confidence that actions in one part of the owl’s range would not greatly affect other populations.

Keitt et al. (1995; and refined by Keitt et al. 1997) reported that patches of forest habitat in the range of the Mexican spotted owl showed a connectivity threshold of approximately 45 km (28 mi). They concluded that an organism capable of dispersing a distance of ≥45 km (28 mi) through inhospitable terrain, and with an average exponential dispersal distance of ≥15 km (9.3 mi), would perceive the landscape as a series of connected patches. They further concluded that Mexican spotted owls met these criteria (see Dispersal, above), and that the distribution and temporal dynamics of this subspecies’ populations probably behaves as a classical metapopulation over much of its range. That is, the level of 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 SRM 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. This finding suggests that habitat connectivity should be maintained (or increased) across the owl’s range. Habitat connectivity buffers a population from stochastic variability through time by providing the opportunity for local population failures to be “rescued” by immigration from other populations, and it also facilitates gene flow among populations (Barrowclough et al. 2006).

Gutiérrez and Harrison (1996) noted two other concepts related to metapopulation dynamics that are relevant to spotted owls. The first is spatially structured population dynamics. The spatial structuring described by this concept arises from territorial behavior and is relevant in continuous or relatively continuous habitat. Individuals in such habitat will tend to interact mainly with neighboring owls, rather than mixing freely throughout the larger population. The dynamics of this situation can be modeled using individual territory models (Lande 1987, 1988, Noon and McKelvey 1996). Resulting models are similar to metapopulation models, except that extirpation and colonization is modeled for territories rather than for larger populations (Gutiérrez and Harrison 1996, Noon and McKelvey 1996). No individual territory models have
been developed for the Mexican spotted owl. The approach may be relevant to particular areas where clusters of owls occur in relatively continuous habitat, however (e.g., Mogollon Rim, Sacramento Mountains).

The second concept relates to source-sink dynamics (Pulliam 1988). As typically defined, source populations occur in high-quality habitat and produce surplus individuals. In contrast, low quality habitats may act as population sinks, where reproduction is insufficient to balance fatality. Sinks may be occupied only when high quality habitat is fully occupied, in which case sinks can serve a valuable function by serving as a reservoir for surplus individuals (Pulliam 1988, see also Howe et al. 1991). Conversely, if dispersing individuals settle in sinks rather than continuing to search for higher quality habitat, sinks may be detrimental to long-term population viability (Lamberson et al. 1992, Zimmerman et al. 2003).

Little is known about potential source-sink dynamics in Mexican spotted owls. Ganey et al. (2005) reported an example of possible source-sink dynamics in two populations occupying different habitats in the Sacramento Mountains, New Mexico. However, this was based on a study of short-duration involving relatively few owls. Consequently, we cannot be certain that the apparent sink functions as a sink over longer time frames. And, if it is indeed a sink, we do not know whether it serves as a reservoir for surplus owls when population levels are high, or as an ecological trap for individuals that might find better vacant habitat if they continued looking.

Another important concept relevant to metapopulation dynamics deals with correlation (or lack thereof) among population growth rates of different subpopulations. LaHaye et al. (1994) demonstrated that high correlation in vital rates among subpopulations increased the risk that such populations would decline simultaneously. In contrast, lack of correlation among subpopulations resulted in situations where some populations were able to contribute surplus individuals to declining populations. The metapopulation dynamics evaluated were very different for these situations, with increased correlation among subpopulations resulting in an increased risk of rangewide population declines and ultimately extinction.

The extent of correlation in vital rates among subpopulations of Mexican spotted owls is only partly understood. Spotted owl vital rates appear to be partly influenced by large-scale climatic patterns (Seamans et al. 2002, Gutiérrez et al. 2003). Such patterns are likely to be at least somewhat correlated across much of the range of the owl, suggesting that correlation among subpopulations could be high. However, available evidence suggests that one vital rate, reproductive output, was only moderately correlated among three populations (Sacramento Mountains, Coconino, and Gila) of Mexican spotted owls during a period of simultaneous study (1991-2000). Reproductive output was relatively high for all populations in 1991. Reproduction in the Sacramento Mountains declined steadily to low levels and remained there through 1995, rebounding in 1996 (Ward 2001: Fig. 3.8). Reproduction was more variable in the other two populations, but declined abruptly in both from 1993 to 1994 (Seamans et al. 1999: Fig. 2). Reproduction in the Coconino population then increased gradually from 1994 to 1996, whereas reproduction in the Gila population continued to decline through 1995 before rebounding in 1996. Thus, reproduction appeared to be somewhat, but not completely, correlated in these populations, with a period of low reproduction occurring in all populations during the mid-1990s. This decline occurred earlier in the Sacramento Mountains (BRE EMU) than in the other
two populations. However, the Coconino and Gila populations both were located in the UGM EMU, and climatic patterns (and therefore population dynamics) may be more similar within than among EMUs. Survival estimates also are available for two of these populations during the same time period (Seamans et al. 1999: Fig. 3). Survival trajectories were similar between areas for owls <1 year old, but not for older owls. Again, this suggests some level of correlation in vital rates among populations but that such rates are not completely correlated among populations.

In summary, the distribution of Mexican spotted owls throughout their range suggests a spatial distribution congruent with a group of subpopulations that may function as a metapopulation. The UGM EMU includes the largest contiguous area of habitat for Mexican spotted owls, which is reflected in the large number of documented owls in that EMU (e.g., Ganey et al. 2004, see also Table B.1). Because of its size and central location to other areas inhabited by Mexican spotted owls, the larger subpopulation in this EMU likely serves as a core, source population for supplying new recruits to proximal outlying locations. Other subpopulations, particularly those occurring in the BRE, appear isolated enough that recruitment must come primarily from reproduction within the local subpopulation. Limited evidence from simulation models and genetic analysis supports these aspects of metapopulation function and spatially structured population dynamics. Although temporarily asynchronous reproduction and survival may occur among some subpopulations, interstitial distances and dispersal ability may limit the beneficial traits of metapopulation function such as the numerical rescue effect. This may be the case for the concentrated population of Mexican spotted owls in the Sacramento Mountains of New Mexico (Barrowclough et al. 2006). Consequently, subpopulations that are large enough to produce surplus individuals (i.e., acting as a source population) in some years, but isolated enough that external recruitment is rare, will require more conservation attention to maintaining internal recruitment and viability; whereas conservation for smaller subpopulations near larger core populations may require a greater focus on identifying and enhancing dispersal corridors. More information is needed to identify the magnitude of numerical exchange of individuals among subpopulations and the relative influence on local, EMU-wide, and rangewide population viability.

9. Conclusions

In many ways, the Mexican spotted owl appears to be quite similar to both the northern and California spotted owls with respect to general behavioral patterns and ecology. For example, all three subspecies are most common in forests of complex structure, prey mainly on nocturnally active small mammals, and share similar vocalizations, reproductive chronologies, and population characteristics. However, important differences exist between the Mexican spotted owl and the other subspecies. The distributional pattern of the Mexican spotted owl is more disjunct and ranges over a much larger area than that of the other subspecies, with the possible exception of some California spotted owl populations that occur in disjunct mountain ranges of southern California (Noon and McKelvey 1992). The Mexican subspecies also appears to use a wider range of habitat types than the other subspecies and to date only the Mexican subspecies has been found to dwell and reproduce in rocky canyons in any significant numbers (although cliff nesting has been documented in both northern [Hane et al. 2007] and California [Peyton 1910, Dickey 1914] spotted owls). These unique aspects of the ecology of the Mexican spotted
owl require unique approaches to its management. For example, threats to owl habitat and management proposed to address those threats may well differ among the diverse habitats occupied by Mexican spotted owls. In addition, because of its disjunct distributional pattern, dispersal among subpopulations of Mexican spotted owls is an important consideration. Thus, habitat management plans may need to consider not only areas occupied by owls but also intervening areas, even where such areas are very different in habitat structure from those typically occupied by Mexican spotted owls.

We have learned a great deal about the Mexican spotted owl in the last three decades, but significant information gaps still remain. Most studies of the owl to date have been descriptive rather than experimental. Although we have identified patterns with respect to some aspects of this owl’s ecology (e.g. habitat use), cause and effect relationships have not been documented. Much more information is needed on how specific factors alone and in combination affect change in Mexican spotted owl abundance. These considerations suggest that much additional research is needed, and that management recommendations in the near term must deal with extremely high levels of uncertainty.