

Chapter 4

The California Spotted Owl: General Biology and Ecological Relations

Jared Verner, R. J. Gutiérrez, and Gordon I. Gould, Jr.

Understanding a species' ecology and life history and its role in ecosystem functions is vital to successful management of that species. The extent to which this understanding is comprehensive and correct is also critical. This chapter emphasizes life history elements and ecological relations of the California spotted owl that bear directly on planning for its management. In that sense, this is not an extensive, detailed treatment of the owl's biology and ecology. Nor does it provide a thorough analysis of some of the primary factors that must be considered, such as habitat relations, home ranges, density, and demography. Instead, because these components are so critical to conservation planning, and each requires extensive analyses, other chapters treat them in considerable detail.

Description and Classification

The spotted owl is generally mottled in appearance, the back is brown with irregular white spots and the underparts distinctly lighter, with white spots and brown barring. The facial disk is pale brown with concentric rings of darker brown and bordered by a ring of dark brown feathers. Pale "eyebrows" and "whiskers" merge into a conspicuous, light-colored "X" between the eyes and above the beak. Unlike most other owl species, which have yellow eyes, the eyes of spotted owls are dark brown. The beak is pale yellowish. Wings and tail are rounded and all flight feathers are dark brown with light-brown crossbars. The legs and toes are fully covered with short, pale-buff feathers, and the claws are dark brown to black. Adult males and females cannot be distinguished by plumage (Forsman 1981), but they are readily identified by voice and size (Forsman et al. 1984, Blakesley et al. 1990). Barrows et al. (1982) indicated that sexes can be distinguished by the number of tail bars, but Blakesley et al. (1990) found this characteristic to be unreliable. Moen et al. (1991) noted that first-year and second-year adults can be distinguished by the shape of the tips of their tail feathers.

Only four of the 19 species of owls occurring in North America are larger than the spotted owl (Johnsgard 1988). Based on live weights from a sample of 46 adult male and 48 adult female California spotted owls captured in the Sierra National Forest (NF) and Sequoia National Park (NP) (Steger pers. comm.), females averaged 22.2 ounces-13.6 percent heavier than the

average of males at 19.6 ounces. Weights of individuals captured more than once differed markedly, which is not surprising considering that some common prey items of spotted owls (for example, woodrats) weigh as much as a third of an adult owl's weight. For comparison, live weights of 65 female northern spotted owls captured in northwestern California averaged 23.2 ounces; 68 males averaged 20.3 ounces (Blakesley et al. 1990).

The American Ornithologists' Union (1957) recognized three subspecies of the spotted owl-California spotted owl (*Strix occidentalis occidentalis*) (Xantus 1859), northern spotted owl (*Strix occidentalis caurina*) (Merriam 1898), and Mexican spotted owl (*Strix occidentalis lucida*) (Nelson 1903). The Mexican form, found from southern Utah and Colorado southward into Arizona, New Mexico, and Mexico, is geographically isolated from the California and northern subspecies. The California spotted owl is confined to the State of California (figs. 4A, 4B, and 4C), where its distribution in the southern Cascade Mountains adjoins a south-eastern extension of the range of the northern spotted owl. This contact zone is along the Pit River, east of Redding.

Barrowclough (pers. comm.) has observed north-south clinal variation (gradual change) in morphology of northern and California spotted owls. Barrowclough and Gutierrez (1990) found no electrophoretic differences between the northern and California subspecies, so their study shed no light on the question of a taxonomic distinction. As in other such studies, however, only a fraction of the total genetic information was compared. The American Ornithologists' Union has consistently recognized two subspecies of spotted owls in California; this position was recently reaffirmed (N. K. Johnson pers. comm.).

Questions about whether the northern and California spotted owls are valid subspecies, however, are essentially irrelevant to concerns about the status of the owls. Spotted owls certainly move back and forth across the Pit River, and interbreeding between northern and California forms undoubtedly occurs in that area. Subspecies, by definition, are not reproductively isolated from each other. The important management questions relate to conditions of populations and habitats in various parts of the spotted owl's overall range, not to details of its subspeciation. The owl may be doing well in some areas but not in others. Where it is not doing well, we need to consider options for improving its status. Generally, this will involve improving habitat conditions and increasing the crude densities of owls to increase the efficiency of dispersal (Chapters 8 and 9). Maintaining the continuity of spotted owl populations from the northern Sierra Nevada into the southern Cascades and northwestern California is an important part of assuring the overall viability of both subspecies (Dawson et al. 1987, Thomas et al. 1990).

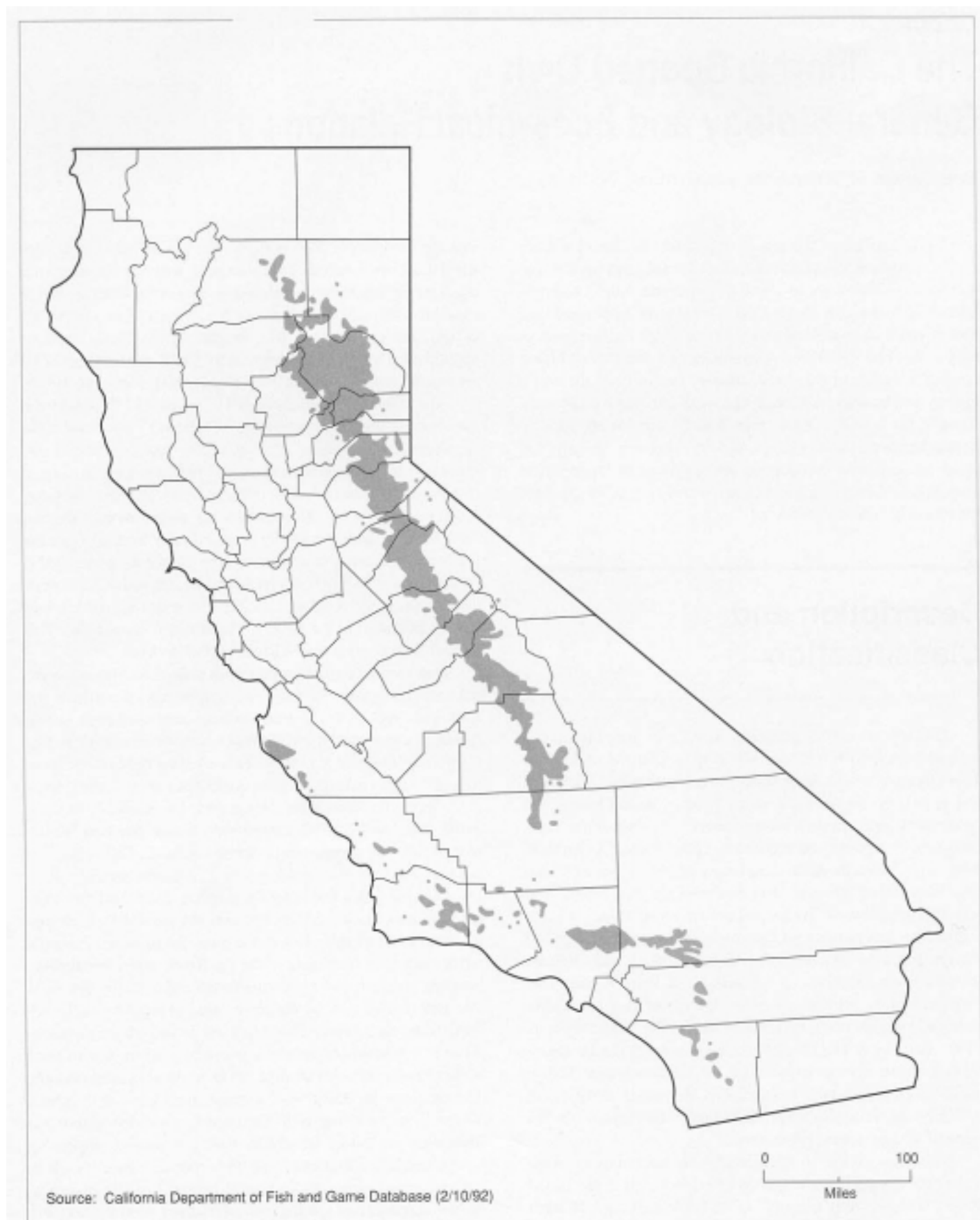


Figure 4A-Distribution of California spotted owls.

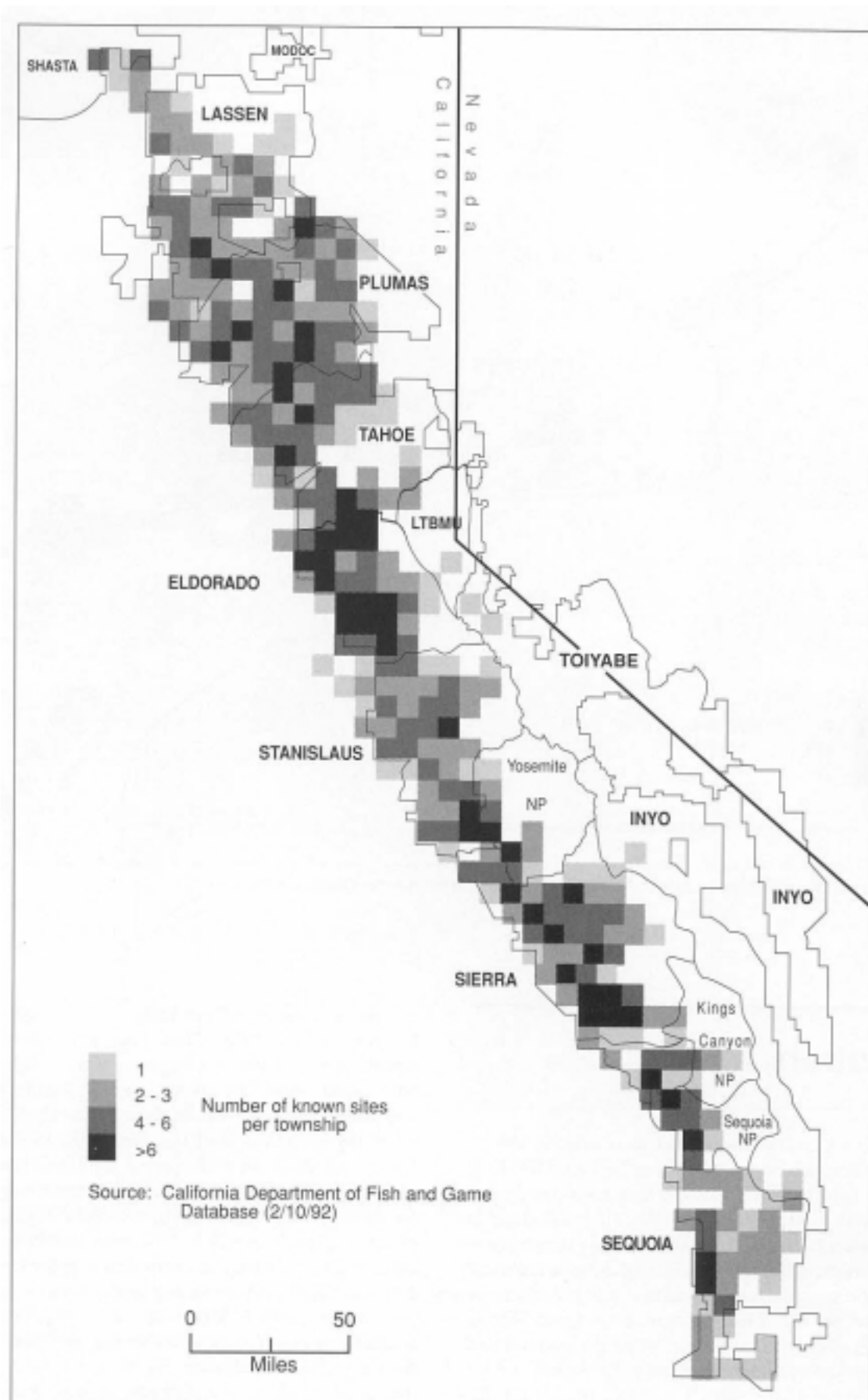


Figure 4B—Detail of the relative abundance of California spotted owls in the Sierra Nevada Province.

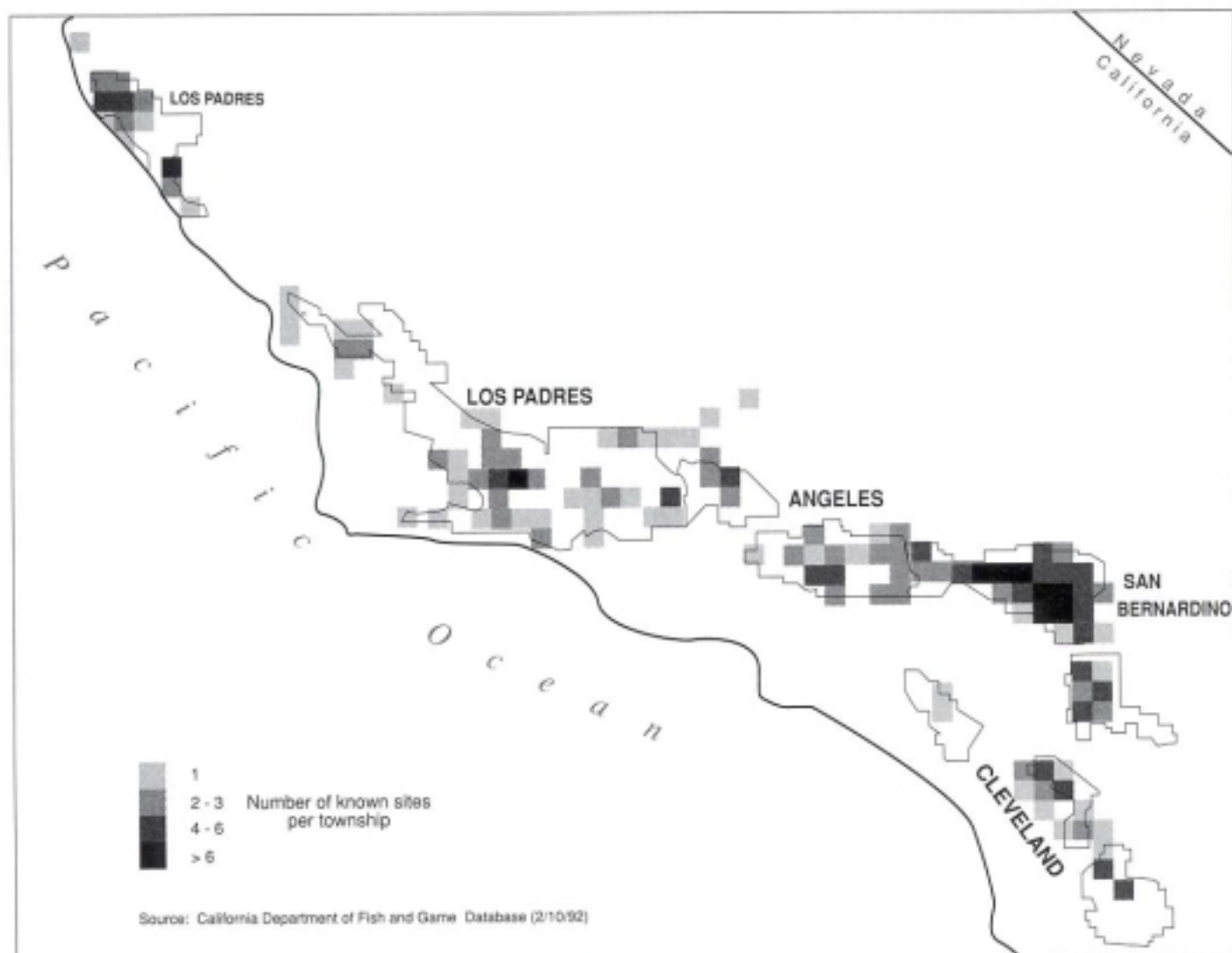


Figure 4C-Detail of the relative abundance of California spotted owls in the Southern California Province.

Distribution

The California spotted owl occurs in coniferous forests, mixtures of conifers and hardwoods, and in hardwood forests in the western Sierra Nevada; few locations have been documented east of the Sierran crest (figs. 4A and 4B). They also occur in conifer, conifer/hardwood, and hardwood stands in mountainous country of southern California, and in coastal mountains and foothills from the Santa Barbara area north at least into Monterey County (figs. 4A and 4C). Most owl pairs in the Sierra Nevada occur in the mixed-conifer forest type, but in the mountains of southern California they are almost equally represented in three major habitat types-mixed-conifer, live oak/bigcone Douglas-fir, and riparian/hardwood (tables 3A and 3I) (habitat types are described in Chapter 1 and Appendix B).

Areas in the coastal mountains north of Santa Cruz appear to have suitable habitats. These have not been inventoried adequately for owls, but they appear similar to others in the State where spotted owls are known to breed. Finally, spotted owls may also occur in denser stands of riparian/hardwood forests, especially in foothills bordering eastern portions of the Central Valley and along the south-central California coast (fig. 4D). The potential spotted owl habitat in lower-elevation hardwood forests depicted in figure 4D includes habitat within the ranges of both the northern and the California spotted owl. It encompasses about 5,000,000 acres, of which about 1,100,000 acres are rated "high" as potential owl habitat (Greenwood and Steger pers. comm.), with 625,000 acres of the high-potential habitat within the range of the California spotted owl. Essentially none of this has yet been surveyed for spotted owls, so we cannot estimate the number of pairs, if any, that may be located there. Obviously surveying these habitats, on a sample basis, is a priority need.



Figure 4D-Statewide distribution of potential California spotted owl habitat in lower-elevation hardwood forests.'

Habitat Associations

Quantitative details about habitat associations of California spotted owls are given in Chapters 5, 6, and 7. Generally, however, the birds occur only in habitats with substantial tree cover and especially with some larger, older trees present (see the set of color photos at the end of Chapter 5).

Nesting Habitat

Habitats used for nesting typically have greater than 70 percent total canopy cover (all canopy above 7 feet), except at very high elevations where canopy cover as low as 30-40 percent may occur (as in some red fir stands of the Sierra Nevada). Nest stands typically exhibit a mixture of tree sizes and usually at least two canopy layers, and some very large, old trees are usually present. Often these have large, natural cavities, broken tops, and/or dwarf mistletoe brooms. Nest stands in conifer forests usually have some large snags and an accumulation of fallen logs and limbs on the ground; downed woody debris is not a major component of nest sites in lower-elevation riparian/hardwood forests.

Spotted owls do not build their own nests but depend mainly on finding a suitable, naturally occurring site. Nest heights vary regionally—about 38 feet in riparian/hardwood forests at lower elevations; about 65 and 57 feet in conifer forests of the northern and southern Sierra Nevada, respectively; and about 58 feet in conifer forests in the San Bernardino Mountains (table 5K). In Sierran conifer forests, nests are usually in cavities or on broken-topped trees or snags. Less often they are on platforms associated with abandoned raptor nests, squirrel nests, dwarf mistletoe brooms, or debris accumulations in trees (Chapter 5). LaHaye (1988) found an increase from north to south in the proportion of platform nests used by northern spotted owls in a study in northwestern California. Similarly, cavity nests dominate nest types of California spotted owls in the Sierra Nevada, but platform nests predominate in the San Bernardino Mountains (table 5I). These trends probably reflect the distribution of stand ages rather than latitude.

Nest trees (details in Chapter 5) are typically large [mean diameter at breast height (d.b.h.) of about 45 inches for nest trees in Sierran conifer forests and 37 inches in the San Bernardino Mountains] and decadent. Among 124 nests found on NFs in the Sierra Nevada, 34 were in snags and 90 were in live trees. Eighty-two (66.1 percent) were in cavities and 19 (15.3 percent) were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions all tend to develop in older trees. Only 17 (13.7 percent) of the nests were on stick platforms built and used previously by other species (probably including goshawks, sharp-shinned hawks, ravens, and tree squirrels). Some owl pairs use the same nest cavity or platform repeatedly from year to year, some select new sites each year, and yet other alternate nest sites over time (Foreman et al. 1984, p. 31; R. J. Gutiérrez pers. observ.; LaHaye pers. comm.).

The species of nest trees used seems to depend on what is available, with 10 species of conifers and 7 species of hardwoods accounting for all nests in our database (table 5J). Locations of nest trees in the Sierran sample ranged in elevation from 1,000 to 7,740 feet, with 86 percent found from 3,000 to 7,000 feet in elevation. The highest elevation of nests increased from the northern to the southern Sierra Nevada (Lassen NF - 6,400, Plumas NF - 6,100, Tahoe NF - 7,000, Eldorado NF - 6,340, Stanislaus NF - 7,200, Sierra NF - 7,500, and Sequoia NF - 7,740 feet). The distribution of breeding spotted owls in the Sierra and Sequoia NFs extends down at least to 1,000 feet in elevation (Neal et al. 1989). The lower elevation of the study area with nests at 1,000 feet is bounded by a reservoir, so owls elsewhere may nest at even lower elevations. Few surveys have been done at these lower elevations. In southern California, nests ranged in elevation from 1,000 feet (Los Padres NF) to 8,400 feet (San Bernardino NF). The mean elevation of nest sites in the San Bernardino Mountains was about 6,000 feet.

Roosting Habitat

Stands used for roosting are similar to those used for nesting, with relatively high canopy cover, dominated by older trees with large diameters, and with at least two canopy layers. Studies of roosting northern spotted owls indicate that they respond to variation in temperature and exposure by moving higher or lower within the canopy, or around the roost tree, to access more comfortable microclimates (Barrows and Barrows 1978, Forsman 1980, Barrows 1981, Solis 1983, Forsman et al. 1984). The structure of multistoried stands characteristic of roost sites facilitates this movement. This observed response led Barrows and Barrows (1978) to propose that old-growth forests are necessary for spotted owls to avoid heat stress. Based on the following observations, however, we doubt that avoidance of heat stress is an essential benefit of old-growth forests: (1) California spotted owls are relatively common in riparian/hardwood forests in southern California and the Sierran foothills, where ambient temperatures are high during summer months. (2) A female nested in full sunlight on an abandoned Cooper's hawk nest platform in the Sierran foothills. While incubating, she was sometimes exposed to ambient temperatures exceeding 100 degrees Fahrenheit, and the developing young experienced like conditions (Steger pers. comm.). (3) Adult California spotted owls often roost in full sunlight or high in the canopy on hot days, which is not typical of northern spotted owls (R. J. Gutiérrez pers. observ.). We agree that the birds probably move about in a forest canopy to find a comfortable microclimate, but they seem to be able to tolerate relatively high ambient temperatures.

Foraging Habitat

Foraging habitats include suitable nesting and roosting sites, as well as more open stands, regularly down to 40-50 percent canopy cover, that are generally similar in structure and composition to nesting and roosting habitat. Typical conditions in conifer forests include:

1. A mixture of tree sizes, usually with some trees exceeding 2 feet in d.b.h., resulting in tree canopies at a wide range of heights in a stand but not necessarily in distinct layers. (Many sites depicted in the color photos at the end of Chapter 5 were taken in areas where spotted owls were known to forage.)
 2. Signs, of decadence-snags, overmature trees, downer woody debris (large logs are especially characteristic).
 3. The presence of hardwoods probably tends to enhance foraging habitat in conifer forests.
 4. Ample open flying space within and beneath the canopy
- Conditions in foraging habitat in hardwood stands in southern California, and at lower elevations in the Sierra Nevada, tend to have less downed woody debris than found in conifer forests and stands tend not to be multilayered. Because woodrats dominate the diets of owls in these hardwood habitats, we can infer that they provide good habitat for woodrats as well. Live oaks are common in the canopy and a variety of shrubs provide food (leaves, buds, flowers, and so on) for woodrats (Chapter 10).

Home Range and Territoriality

Spotted owls generally have large home ranges, defined by Thomas et al. (1990, p. 419) as "the area to which the activities of an animal are confined during a defined period of time." By contrast, an animal's "territory" is generally a defended area (Nice 1941) within its home range. Home ranges of radio-tagged, neighboring spotted owls overlap to varying degrees (reviews in Thomas et al. 1990, appendix I; Carey et al. 1992; Chapter 6). Observations by Forsman et al. (1984, p. 52-53) indicate that aggression between neighboring birds is infrequent, apparently confined to interactions between members of the same sex, and generally more pronounced when an intruder is well within the home range of another bird. These observations suggest a form of territoriality in which "...an individual or a pair may be dominant in the core area of its home range but not in the periphery. This tends to produce a regular dispersion by effectively excluding other individuals from breeding in the core without necessarily excluding their presence there as subordinates engaged in other activities" (Brown and Orians 1970, p. 244).

Median, combined home ranges of members of pairs of northern spotted owls, estimated from radio-tagged birds and using minimum convex polygons as the estimator, ranged from 1,411 acres in the South Umpqua River Valley in the Klamath Mountains of southwestern Oregon to 9,930 acres on the Olympic Peninsula in northwestern Washington (Thomas et al. 1990, p. 194). Home ranges were generally larger in Washington than in areas to the south. In Oregon, areas where median pair home ranges exceeded 5,000 acres were usually in heavily logged sites with a low percentage of the landscape covered by older forests

(Forsman et al. 1984, Carey 1985, Thraillkill and Meslow 1990). Home ranges of the California spotted owl exhibit similar variation in size, being measured in thousands of acres in higher-elevation conifer forests but only in hundreds of acres in foothill woodlands of the Sierra Nevada (Chapter 6). We strongly suspect that prey availability accounts for a major part of the variation in home-range size of the spotted owl (see discussion below in section entitled "Why Differences in Home-Range Size?").

As in other bird species, some spotted owls do not exhibit fidelity to an area, their movements indicating instead that they do not occupy a specific home range (Chapter 6). Juveniles often wander widely in search of a vacant home range, and similar behavior may occur among adults displaced for some reason from their former home range. They may move within or among the home ranges of other birds, where they await opportunities to join the breeding population when a territorial owl dies or deserts its territory. These birds are referred to as "floaters" by ornithologists (Smith 1978, 1984). Their role in avian population dynamics is believed to be critical (review in Thomas et al. 1990, p. 295; Franklin 1992), but less is known about them than any other subset of bird populations. This is true because floaters are typically quiet and secretive, avoiding contact with territorial birds and being less susceptible to detection by researchers. For these reasons, we have no quantitative information on the ratio of floaters to territorial birds in any population of spotted owls.

Vocalizations

Spotted owls communicate with a variety of hoots, "barks," and whistles (Forsman 1976, Forsman et al. 1984). The context of some of these calls is unknown, but researchers generally agree on the function of some of the more common calls. For example, the most common call is the four-note hoot, phonetically described as "hooo---hoo-hoo---hooooo." It advertizes the fact that an owl is on its territory and probably functions both to repel intruders and to attract potential mates. Given at a lower pitch and intensity, this same call is also used by the male to announce prey delivery to his mate, and in other sexual interactions. Owl biologists most often imitate this call when attempting to locate or attract spotted owls in the field.

Another common call is the multiple-note "series," which is a highly variable rendition of the basic four-note hoot (Fitton 1991). It is used by birds in an excited state. Spotted owls also produce whistles that usually serve to maintain contact between members of a pair (Forsman et al. 1984). The calls of females are higher-pitched than those of males, facilitating identification of sexes in the field. Calls of spotted owls also vary spatially and temporally (Ganey 1990, Fitton 1991).

Pair Bond

All available evidence indicates that spotted owls are monogamous. Forsman et al. (1984, p. 53) concluded that pair bonds are usually maintained from year to year primarily because (1) individuals of both sexes tend to remain within their home ranges, and (2) they tend to exclude other individuals of the same sex from their home ranges. Owls that remain throughout the year in the same home range generally maintain a solitary existence during the nonbreeding period, seldom even roosting near their mates. Mate constancy, therefore, may be "more a function of the attachment to a traditional home range than attachment to a particular mate." Observations of migrant spotted owls support this conclusion. Mates do not migrate or spend the winter months together. Survivors return to their former summer home ranges, where former pair bonds are renewed if both members of the pair survive (Verner et al. 1991).

Not all pair bonds last for as long as both members of the pair survive, however. "Divorces" have been observed in several demographic studies of spotted owls, but they are rare and reasons for them are unknown (R. J. Gutiérrez pers. observ., LaHaye pers. comm., Steger pers. comm.). When an owl of either sex loses its mate, it may desert its old home range and form a new pair bond elsewhere; it may remain on the old home range and acquire a new mate there; it may remain unmated for an extended period of time; or it may become a floater. Too few instances have been observed to identify a pattern, although LaHaye suspects that females that lost mates left their old home range more often than was the case for males in his study in the San Bernardino Mountains.

The Annual Cycle

Knowledge of the owl's annual cycle is essential for delineating any restrictions on projects and activities that might be planned within owl territories. The following account of the spotted owl's breeding chronology is drawn mainly from Forsman et al. (1984), who have provided the best quantitative information. Although it is based primarily on observations of pairs, nests, and broods of the northern subspecies in Oregon, we believe it is the same or similar for the California spotted owl. Estimated periods for the different stages of the cycle were based on unpublished information and summaries provided by National Forest biologists; by Blakesley (pers. comm.) and Steger (pers. comm.) for the Sierra Nevada; by LaHaye (pers. comm.) for the San Bernardino Mountains; and by Stephenson (pers. comm.) for owls at lower elevations in southern California.

Available evidence indicates that spotted owls are physiologically capable of first breeding at the age of 2 years (Barrows 1985, Miller et al. 1985), although rare cases of nesting by yearlings are known (LaHaye pers. comm., Steger pers. comm.). Determining the "usual" age at first breeding is complicated by the fact that nesting by the owls does not occur annually, even among older birds. As a result, a bird that has attained reproductive maturity may not nest for one or more years beyond that age, probably for ecological reasons.

Here and elsewhere in this assessment we recognize five stages of the breeding cycle—prelaying, laying, incubation, nestling, and fledgling. The timing of these stages (fig. 4E) is especially important information for management purposes. Because not all birds begin nesting at the same time, the duration of each stage for all owls in a region, such as the conifer forests of the Sierra Nevada, is considerably longer than it is for a single pair.

The breeding cycle of California spotted owls extends from about mid-February to mid- or late September or early October, when young are no longer cared for regularly by their parents (fig. 4E). The cycle apparently begins earlier in some places than in others in a given year. For example, Steger (pers. comm.) believes that spotted owls in the foothills of the Sierra Nevada initiate breeding about 2 weeks earlier than birds in the higher conifer forests at the same latitude. The various stages tend to begin about 4 days earlier in the San Bernardino Mountains than in the conifer zone of the Sierra Nevada (fig. 4E). As in the Sierra Nevada, timing at lower elevations in southern California apparently precedes that in the San Bernardino Mountains by about 2 weeks (Stephenson pers. comm.). Reasons for these differences may be related to local differences in peak periods of prey abundance for the owls. Before this can be determined, however, much more information is needed to refine details of the owl's breeding cycles and periods of prey abundance in all localities.

Prelaying Stage (duration variable) (see Forsman et al. 1984, p. 34)

Members of nonmigrating pairs generally do not roost together during the winter. By late winter, however, they increasingly roost together, engage in mutual preening, and occasionally copulate in the evening. For 2 weeks or so before the date of first laying, paired birds typically roost together every night and copulate once or twice each evening. Beginning about a week before laying, the female spends most of her time near the nest, receiving an increasing share of her food from the male. These activities probably do not last as long for birds that migrate, because members of migrant pairs spend the winter in different locations and do not return to their breeding territories until shortly before laying begins. Because the prelaying stage has no clearly definable beginning, we have arbitrarily designated the 3 weeks prior to laying of the first egg as the prelaying stage.

Laying Stage (1-6 days)

Data suggest that the peak laying period probably occurs from about 7 to 21 April in the San Bernardino Mountains and from about 11 to 25 April in conifer forests of the Sierra Nevada. When egg laying begins, a female spotted owl spends almost all



Figure 4E—Chronology of the breeding seasons of California spotted owls in conifer forests of the Sierra Nevada and the San Bernardino Mountains.

of her time in the nest, and her mate provides nearly all of her food. Copulation continues on a daily basis throughout the egg-laying stage and for up to about 4 days after incubation begins.

The clutch size of the spotted owl is one of the smallest among North American owls (Johnsgard 1988). Most clutches contain two eggs; three-egg clutches are infrequent and four-egg clutches are rare (only two records—Bendire 1892, Dunn 1901). The interval between laying of successive eggs is 72 ± 6 hours (Forsman et al. 1984, p. 33), so the laying period would be 1 day for a clutch of one egg, 3 days for a clutch of two, and 6 days for a clutch of three. (A rare clutch of four eggs would presumably stretch the laying period to 9 days.)

Incubation Stage (30 ± 2 days) (Forsman et al. 1984, p. 33)

Incubation begins shortly after laying of the first egg and is done solely by the female, who may leave the nest at night for periods up to 2 hours during the first 2 days of incubation. Thereafter, she only occasionally leaves the nest for periods of 10 to 20 minutes at night to regurgitate pellets, defecate, preen, or accept food from her mate. The female does not forage during the incubation period, receiving all her food from her mate. The male typically roosts within 650 feet of the nest during the daytime and begins to forage shortly after sunset (Forsman et al. 1984, p. 35).

Coincident with the laying of eggs, the female develops a brood patch—"a feather-free area with thickened skin and a rich supply of blood vessels to facilitate the transfer of heat from the body of the incubating bird to the eggs" (Pettingill 1970, p. 355). The presence of a well-developed brood patch is clear evidence that a female has been incubating.

Nestling Stage (normally 34-36 days) (Forsman et al. 1984, p. 37)

The peak hatching period probably occurs from about 3 to 17 May in the San Bernardino Mountains and from about 7 to 21 May in the conifer zone of the Sierra Nevada. The female broods the new hatchlings almost continuously for 8-10 days, still depending on her mate to provide food for herself, and now for the young. By the time her young are 2-3 weeks old, the female begins to forage for increasingly longer periods at night—typically 1-4 hours. The male continues to bring food to the nest, but the female then passes the food to the young. Apparently the male seldom, if ever, passes food directly to nestlings. Forsman et al. (1984, p. 35) reported that they never observed males feeding nestlings. If the male brings food to the nest while the female is away, he simply leaves it in the nest. The female continues to roost in the nest until 3-6 days before the young leave it.

Most young observed by Forsman et al. (1984) fledged (left the nest) when 34-36 days old, occasionally moving off the nest to perch on nearby limbs for a few days before leaving the nest permanently. Occasionally young leave their nest earlier than normal. Because such young are less developed physically, they may spend more time on the ground than young that remain in the nest for the full nestling period. This may increase their mortality rate compared to that of later-fledging young (Forsman et al. 1984, p. 36).

Fledgling Stage (80-120 days) (Forsman pers. comm.)

The fledgling stage covers the period after the young leave the nest until they become independent of their parents. The

peak period of fledging probably occurs from about 8 to 22 June in the San Bernardino Mountains and from about 12 to 26 June in conifer forests of the Sierra Nevada. New fledglings are weak fliers, often falling to the ground, where they may spend several hours to several days. Within about 3 days after fledging (assuming a normal nestling period of 34-36 days), most young can flutter or climb to elevated perches; usually in a week they can fly clumsily between trees. Within about 3 weeks after fledging, they can hold and tear meat from prey brought by their parents (Forsman et al. 1984, p. 37). Although adult males bring food for the fledglings at all ages, they generally do not give the food directly to the young until they have been out of the nest for at least 2 weeks (Forsman pers. comm.). Both parents regularly bring food to the fledglings and generally continue to do so until mid- to late September, apparently regardless of the age or capabilities of the young. Because of this, the fledgling stage may be relatively long or short, depending upon when a given nest was begun and on variations in the age of the young at fledging.

The Nonbreeding (Winter) Period

Activities of spotted owls during this period are primarily related to basic maintenance-capturing prey, securing protection from the elements, avoiding predators, preening; and so on.

The beginning of the nonbreeding period is technically the date when adults quit feeding their young, although this may not be well-defined because feeding may continue sporadically even well after the young can capture and kill prey for themselves. Three changes in owl status indicate that 1 October is a reasonable beginning of the nonbreeding period in the Sierra Nevada, at least for most birds: Young are generally independent of their parents by late September; juveniles begin dispersal as early as 1 October (Laymon 1988); and some adults begin fall migration early in October (Laymon 1988, Neal et al. 1989). The end of the winter period coincides with the beginning of activities characteristic of the prelaying stage. This is also a poorly defined date, partly because the initiation of prelaying behavior is not abrupt and partly because timing differs among pairs. Many pairs, however, have initiated prelaying activities at least by the end of February, and egg laying and incubation begin at some nests by the end of March. For planning purposes, therefore, we can reasonably set the end of the winter period at the end of February, at least for most birds.

Movements

Regular, long-distance movements of birds beyond home-range boundaries are of two types-migration and dispersal. Migration is an annual movement between breeding and nonbreeding home ranges. Natal dispersal is the movement of young birds from their natal territory to a site where they breed or at least establish a territory where breeding could occur (Green-

wood 1980). Sometimes adult birds are displaced from established territories by loss of habitat through fire, logging, or other major disturbances. Adults displaced by loss of habitat, or separating from a mate, may begin searching for new territories. Their movement to a new territory is referred to as breeding dispersal.

Migration

Migration is rare among northern spotted owls (Forsman et al. 1984), although a few individuals in the Washington Cascades have moved back and forth several miles between breeding and nonbreeding home ranges without an appreciable change in altitude, latitude, or habitat type (Brewer and Allen 1985). Some radio-tagged California spotted owls in the Sierra Nevada have migrated altitudinally, however, moving downslope for the winter period on the Eldorado NF (Laymon 1988) and the Sierra NF (Neal et al. 1988, 1989, 1990; Verner et al. 1991). At least 8 of 10 birds in Laymon's study left breeding home ranges in mixed-conifer forests (elevations 4,000-5,200 feet) to spend the winter in oak/pine woodlands (elevations 1,000-3,500 feet). The mean elevational displacement between breeding and nonbreeding areas was 2,450 feet; the straight-line distance between areas was 10 to 36 miles (mean = 20). The earliest migrant left its summer home range on 18 October, the latest on 18 November. Dates of return to breeding areas were not determined, because batteries in the radio transmitters failed during the winter. The owls were, however, back in their breeding territories by mid-April.

Six of 18 radio-tagged owls on the Sierra NF migrated from summer home ranges in mixed-conifer forest at 5,700-6,700 feet in elevation to winter home ranges in oak/pine woodlands at 1,100-2,050 feet in elevation. Departure dates ranged from 8 October to 17 December; one female departed her summer home range on 8 October 1987, 8 November 1988, and 20 November 1989. Vertical displacement ranged from 3,680 to 5,541 feet (mean = 4,628) and straight-line distances between areas were 9.6 to 15.3 miles (mean 12.3). Spring return dates ranged from 27 February to 28 March.

None of four owls radio-tagged by Call (1990) migrated during his study on the Tahoe NF (elevations from 2,200 to 5,200 feet), where he tracked from summer through early December in both 1986 and 1987. Call's tracking period in both years lasted well beyond the fall migration dates observed by Laymon, and >2 feet of snow had accumulated in his study area by December of 1986.

No members of any pair in either the Eldorado NF or the Sierra NF study migrated together or established winter home ranges in the same area. In both studies, at least one migrant moved back and forth between winter and summer home ranges once or twice during the winter. Six of the 18 owls in the Sierra NF study whose movements were well-documented were year-round residents, remaining within essentially the same home-range boundaries during summer and winter periods. Two simply enlarged their summer home ranges for the winter period, and five shifted their home range for the winter period but their summer and winter home ranges overlapped. Nine of the 18 were tracked through at least two annual cycles; none of these birds changed behavioral patterns from one year to the next (that

is, once a migrant always a migrant, and so on). The Sierra NF study included another 11 owls that remained as permanent residents in foothill riparian/hardwood forests, at elevations ranging from 1,000 to 4,000 feet. Home ranges of these birds were often shared in winter with migrants from higher elevations.

Data available from these studies thus show individual variation in migratory behavior of the California spotted owl. Collectively, the three studies tracked 32 birds with summer home ranges in the higher-elevation conifer forests long enough to determine whether they did or did not migrate; at least 14 (44 percent) were altitudinal migrants. Because the sample is small, however, we cannot sort out the reasons why some individuals migrated and others did not. Nor can we determine why all 10 owls in the Eldorado NF study migrated, none of the four in the Tahoe NF study migrated, and only about a fourth of the 18 birds in the Sierra NF study migrated. It does not appear to be the case that habitat quality was best in the Tahoe and poorest in the Eldorado study area. Only 35 percent of the Tahoe study area was in stands of large sawtimber (≥ 21 inches in d.b.h.). Because Call (1990) did not report the proportion of the large sawtimber that also had ≥ 40 percent total canopy cover, we assume that something less than 35 percent had both large sawtimber and

suitable canopy cover. The Sierra study area was only about 14 percent large sawtimber (table 6C). On the other hand, the Eldorado study area, with the highest proportion of migrants, was 39 percent in large sawtimber that also had ≥ 40 percent canopy cover (Bias 1989). Finally, in the Sierra study area, some owls left areas for the winter that were subsequently used during the winter by other owls (Steger pers. comm.), suggesting that the birds that left them did so for reasons other than food shortage.

Altitudinal migration may expose owls to added sources of mortality, some related to various human activities. They may cross roadways and be hit by a vehicle. In many lower sites, in foothills of the western Sierra Nevada, traditional wintering areas for the owls are being developed for home sites, even communities. And the development of residential properties, with resulting homes, lawns, driveways, and so on, will eliminate otherwise suitable habitat for woodrats—the staple winter diet of spotted owls in these oak/pine woodlands (table 4A). Finally, foothill woodlands are used extensively to graze cattle and to harvest firewood from oaks. Both of these activities can have negative impacts on woodrat populations and on the cover value of the habitat for owls.

Table 4A -A summary of California spotted owl diets, expressed as estimated percent biomass from different studies.

Diet	Sierra Nevada								Southern California	
									Mixed- evergreen forest	Riparian/ mixed hardwood
	Sierran mixed-conifer forest						Riparian/hardwood woodland			
	Lassen National Forest	Eldorado National Forest		Sequoia/ Kings Cyn. Nat. Prk.					Riverside, San Diego, Orange cos.	Los Padres National Forest
	Spring/ summer	Summer	Summer	Spring/ summer	Spring/ summer	Fall/ winter	Spring/ summer	Fall/ winter	All seasons	Spring/ summer
Woodrats ¹	10.1	35.0	37.5	4.0	8.3	0	73.8	88.0	79.3	93.9
Northern flying squirrel	61.1	24.5	31.3	60.0	50.1	76.6	9.6	0	0	0
Mice ²	1.1	3.0	1.2	1.8	1.5	1.5	1.4	2.6	6.0	1.2
Pocket gophers ³	6.2	1.3	8.1	26.9	20.4	14.7	11.6	5.6	6.0	2.5
Moles ⁴	1.6	4.2	2.0	3.4	3.0	2.1	0.6	0.2	0.2	0
Diurnal squirrels ⁵	4.4	16.5	6.8	4.0	1.9	0	0	0	0.2	0
Lagomorphs ⁶	6.1	0	0	0	0.8	0	0	0	1.0	0
Shrews and voles	2.1	2.4	0.7	0.2	1.2	0.5	1.1	0.6	0.2	0
Bats	<0.1	0.3	0	0.1	0.1	0	Trace	0	0	0.5
Birds	6.7	12.7	12.4	2.7	12.3	4.3	1.9	3.0	7.1	1.5
Insects	0.6	0.1	0.3	0.3	0.5	0.3	0.1	0.1	0.3	0.3
Number of prey items	1,008	1,232	139	162	531	71	234	556	296	30
Elevation (feet)	4,700- 6,800	3,500- 5,000	3,000- 5,500	5,300- 6,900	4,500- 7,000	4,500- 7,000	1,000- 4,500	1,000- 4,500	3,000- 5,500	1,000 3,600
Source	Blakesley (pers. comm.)	Thraillkill Laymon (1988)	Roberts and Bias (1989)	(pers. comm.)	Steger and Eberlein (pers. comm.)				Barrows (1980)	Smith (pers. comm.)

¹ The Lassen sample included both bushy-tailed and dusky-footed woodrats; only dusky-footed woodrats occurred elsewhere.

² Most were white-footed mice (*Peromyscus* spp.), but some samples included minor percentage of pocket mice, jumping mice, or house mice.

³ As many as three species in some samples.

⁴ As many as two species in some samples.

⁵ Included ground squirrels, tree squirrels, and chipmunks.

⁶ The Lassen sample included one pika; all other lagomorphs identified at all sites were rabbits (*Sylvilagus* spp.)

Dispersal

Successful dispersal is essential for population viability. Without it, a population will slowly decline to extinction, because deceased individuals in the breeding population will not be replaced by recruits from dispersing juveniles or adults that have been displaced or have not yet secured a territory. As Miller (1989, p. 1-2) stated, "The distance between adjacent pairs or groups of breeding owls should be such that dispersal of juveniles can replace losses (deaths or emigrations) among existing pairs and provide for colonization of suitable, unoccupied habitats. An understanding of dispersal in juvenile spotted owls is thus basic to formulation of criteria for appropriate spacing of habitat to accommodate pairs of owls." We especially need data on the variability of dispersal distances, dispersal directions, and habitats used by dispersing birds. We also need quantitative information on the extent to which fragmentation of forest habitats impedes successful dispersal (Chapter 9).

Dispersal Among California Spotted Owls

Unfortunately, information on dispersing California spotted owls is nearly nonexistent. Four radio-tagged juveniles on the Eldorado NF (Laymon 1988) initiated dispersal from 1 to 24 October. One was never relocated, another moved 1 mile before it was found dead on 1 December; the others moved straight-line distances of 8.8 and 11.5 miles from their natal sites. This last bird crossed two major rivers and a major highway before settling in oak/pine woodlands near the town of Columbia, at an elevation of 1,300 feet. Two radio-tagged juveniles on the Sierra NF (Steger and Eberlein pers. comm.) moved straight-line distances of 6.1 miles (radio signal lost) and 12.7 miles from their natal areas. The latter bird moved from mixed-conifer forest into oak/pine woodlands. Three color-banded juveniles in the Sierra study dispersed 3.4, 3.5, and 4.1 miles from natal areas to their first territories; four adults banded as members of pairs later shifted territories, moving 2.1, 2.2, 2.4, and 4.4 miles. All of these banded birds were relocated because they stayed within the Sierra NF demographic study area (Steger and Eberlein pers. comm.).

A male color-banded as a fledgling, probably on the Eldorado NF, was found on the Stanislaus NF on 5 September 1990. It was paired and had raised at least one young. This bird was reared in mixed-conifer forest and later paired with a bird in the same forest type. The straight-line distance from its natal home range to its breeding territory was at least 68 miles.

Observations of Dispersing Juvenile Northern Spotted Owls

Because information on dispersal of California spotted owls is so meager, we rely here on studies of dispersal by northern spotted owls to establish quantitative information needed for this assessment. We believe this is a reasonable course of action, because the two subspecies are so closely related that we have no reason to expect dispersal behavior or capability to differ markedly between them.

Over a 4-year period in western Oregon, Miller (1989) fitted 48 juveniles with radio transmitters and monitored their movements regularly. Thirty-two survived to disperse from na-

tal areas (mean = 104 days after fledging). Twenty-seven (84 percent) initiated dispersal between mid-September and mid-October. Their initial movement was usually rapid, and "...most juveniles settled into well-defined areas for their first winter after the initial dispersal movements. Those...surviving their first winter often began moving again in late winter or early spring." From a subset of birds positively identified to sex, males dispersed an average of 16.2 miles (SD = 14.6; $n = 7$) and females an average of 20.4 miles (not significantly different--SD = 6.6; $n = 6$). Initial directions taken by dispersing juveniles did not differ from a random distribution, although six of nine juveniles in 1983 dispersed down the McKenzie River drainage from the H. J. Andrews Experimental Forest. Miller found no significant relation between forest fragmentation and either the final distance moved or the number of days survived by birds in his study. Dispersing juveniles used a wide variety of habitats, but 12 of 18 birds exhibited significant selection for old-growth and mature forests.

In a study of 23 dispersing juveniles in northwestern California (11 in 1983 and 12 in 1984), the birds departed from their natal areas from 22 September to 5 October (Gutiérrez et al. 1985). Dispersing juveniles in 1983 moved a mean of 5 miles per day (range 1 to 11), compared to 1.3 miles per day in 1984 (range 0.8 to 6.4). The difference was statistically significant. Directions taken by dispersing birds varied. They left their natal areas in random directions, with no relation between dispersal direction and the geographic orientation of drainages or ridges. During the first 80 days of dispersal, individuals moved total distances of 15.3 to 92.9 miles ($n = 11$) in 1983 and 0.7 to 62.8 miles ($n = 7$) in 1984. Total distance was the sum of all segments between successive locations as birds were followed during dispersal. Total distance is greater than the straight-line distance between beginning and ending points.

In addition to these more extensive radio-tracking studies of dispersing juveniles, we compiled results from all sources to estimate dispersal distances of radio-tagged juveniles after they left their natal areas (fig. 4F). Only one of the 54 juveniles whose dispersal distances are known was later found as a member of a mated pair, but apparently it never nested (R. J. Gutiérrez pers. observ.). All other birds either died (68 percent), their transmitters failed (27 percent), or they disappeared (5 percent). This raises a question about whether estimates of dispersal distance from radio-tagged birds were biased because the birds were wearing radios. Although radios may have affected their survivorship or their ability to form a pair bond, we found no evidence that distances moved by radio-tagged juveniles were affected by radio transmitters.

If juvenile spotted owls carrying transmitters tended to die sooner than normal, that is, before they dispersed as far as they would without a radio, their dispersal distances might be underestimated. Miller (1989) observed that dispersing juvenile northern spotted owls tended to move quickly from their natal area to a point where they settled for their first winter. Our data set on 54 dispersing juveniles includes a subset of 31 with data on the number of days they dispersed and the number of days they survived thereafter. The dispersal period was highly variable ($\bar{x} = 128.3$ days; SD = 168.5; range = 0-657 days; $n = 31$). The

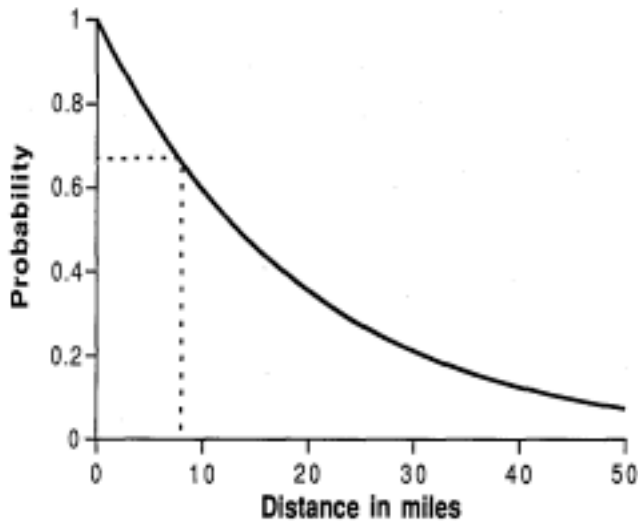


Figure 4F-Probability of dispersing juvenile spotted owls traveling various distances, based on observed dispersal distances of 56 radio-tagged northern spotted owls (Thomas et al. 1990, appendix P). For example, two-thirds of the juveniles would be expected to disperse at least 8 miles (Murphy and Noon 1992).

survival period following dispersal, however, was more consistent ($\bar{x}$ = 119.2 days; SD = 37.4; range = 88-156 days, with one outlier each at 45 days and 284 days). In this subset of 31 dispersers, 13 quit dispersing within 46 days after leaving their natal territory and 11 quit dispersing after at least 83 days (maximum of 657 days). The mean dispersal distances of these two groups were 22.4 miles (SD = 15.7) and 22.0 miles (SD = 8.1), respectively. The correlation coefficient (ρ) between maximum dispersal distance and the number of days dispersed was not significant (r = -0.03; P = 0.88; 95 percent confidence intervals were -0.38 and +0.33; n = 31). The power of the test was 0.37 for ρ = 0.30, 0.61 for ρ = 0.40, and 0.83 for ρ = 0.50. The power for any value of $\rho \geq 0.70$ was 1.0. Consequently, the likelihood of failing to detect a statistically significant correlation that might have had biological significance was slight, and the likelihood of failing to detect a significant ρ of at least 0.70, if one truly existed, was essentially nil.

These results suggest that dispersing juveniles quickly attained their maximum dispersal distance from their natal territory. If they continued to disperse thereafter, their movements tended to keep them within that earlier-attained, maximum dispersal distance.

We also computed the correlation coefficient between maximum dispersal distance and the number of days that juveniles carried radio tags (r = 0.02; 95 percent confidence intervals for the true correlation coefficient were -0.25 and +0.30). ρ was not statistically significant (P = 0.87). The power of the test was 0.60 for ρ = 0.30, 0.86 for ρ = 0.40, and 0.98 for ρ = 0.50. The power for any value of $\rho \geq 0.60$ was 1.0. Examination of scatterplots suggested no patterns that might be missed by just using a correlation coefficient. Additional analyses reported in Thomas et al. (1990, p. 306) corroborate the conclusion from the above results that radio transmitters did not bias estimates of dispersal distance. Lacking critical data from dispersing juvenile California spotted owls, we have therefore used the full data

set on northern spotted owls to estimate dispersal distances of radio-tagged, juvenile spotted owls. The function derived from these data (fig. 4F) was used to parameterize one model for assessing the sensitivity of the southern California metapopulation of spotted owls to various changes in its numbers and distribution (Chapter 9).

Mortality

Birds of most species die of undetermined causes, because they simply are not found in the inconspicuous places where they die. In addition, their bodies are often quickly consumed by other animals in the environment. Spotted owls are no exception. We have little information on their sources of mortality, certainly not enough to establish proportions or even to rank the causes of death. Many dead spotted owls have been examined carefully by veterinarians in an effort to determine the cause of death, but even those examinations are generally unable to pinpoint the exact cause. Instead, a variety of contributing factors is typically suggested. We do know, however, that spotted owls die from the usual variety of causes that befall most wild birds (D. H. Johnson pers. comm.).

Predation

Although spotted owls appear to have few predators, we know that great horned owls and goshawks occasionally capture and eat them: Forsman et al. (1984, p. 38) reported seeing a Cooper's hawk attempt to capture a recently fledged owlet and Forsman and Meslow (pers. comm.) reported one incident of predation by a red-tailed hawk. The great horned owl and the goshawk are both larger than the spotted owl, and all three species often occupy the same forested areas. Great horned owls tend to be more common in areas with lower tree densities than is the case for spotted owls, and the smaller size of spotted owls probably enables them to outmaneuver great horned owls in dense forest. Forsman (pers. comm.) suspects that great horned owls only opportunistically prey on spotted owls.

Goshawks kill both adult and juvenile owls (Gutiérrez et al. 1985, Miller 1989, D. H. Johnson pers. comm.), but spotted owls sometimes nest within goshawk territories and defend their young against attacks by goshawks (R. J. Gutiérrez, pers. observ.). We agree with Forsman et al. (1984, p. 38) that goshawks probably are not serious threats to spotted owls.

Accidents and Starvation

A few deaths from accidents (flying into obstacles, automobiles, and drowning) and starvation have been recorded among spotted owls (for example, Gutiérrez et al. 1985, Laymon 1988, Neal et al. 1988, 1989; R. J. Gutiérrez pers. obser., Forsman and

Meslow pers. comm.). Starvation may result from low abundance or availability of prey, or from lack of hunting experience. Death by starvation is more common among juveniles than adults (Gutiérrez et al. 1985, Miller 1989, Sisco 1990, D. H. Johnson pers. comm.).

Shooting

Shooting deaths have also been documented for spotted owls. For example, both members of a pair of birds that occupied riparian/hardwood habitat in the Switzer Picnic Area in the Angeles NF were shot and killed with "BB" guns by two young boys (Stephenson pers. comm.). This was apparently just a thoughtless act, not a malicious effort to destroy spotted owls, but it does raise a question about the safety of owls in heavily used recreation areas.

Diseases and Parasites

Little is known about diseases and parasites of spotted owls, and nothing is known about the extent to which they contribute to mortality, although Forsman and Meslow (pers. comm.) observed several instances of mortality that they attributed to diseases or parasites. Gutiérrez (1989) surveyed blood parasites in all three subspecies, finding an infection rate of 100 percent, exceeding that recorded in nearly all other bird species (Greiner et al. 1975). Spotted owls must be adapted to these high parasite loads, however, because their survival rates are high even where infection rates are high (Franklin et al. 1990). Hoberg et al. (1989) examined 20 northern spotted owls for helminth parasites and found eight species, representing round worms, flat worms, and spiny-headed worms. More than 80 percent of the birds were infected with at least one species, and multiple infections were common.

Young et al. (1992) reported two species of hippoboscids from northern spotted owls in northwestern California. One species was found only once among the 382 owls examined, but about 17 percent of the owls they examined had hippoboscids infestations of the other species. Fly densities on owls were higher in years with higher summer and fall temperatures and lower winter precipitation. Young et al. (1992) speculated that low temperatures may have depressed survival of fly pupae. In demographic studies in the Sierra NF and Sequoia/Kings Canyon NPs, hippoboscids were detected on 15 of 45 birds (33 percent), but searching for the flies was not an objective of field crews, and limited evidence indicated that the flies were more likely to crawl to the outer surface of an owl when it was handled longer (Steger pers. comm.).

Competition

The barred owl, probably the closest relative of the spotted owl, was historically restricted to eastern North America. Gradually it has extended its range westward through Canada, and finally southward from British Columbia into Washington, Oregon, and more recently into northern California, as far south as the Tahoe NF in the Sierra Nevada (G. I. Gould, Jr., pers. observ.; R. J. Gutiérrez pers. observ.). Barred owls are larger and more aggressive than spotted owls in interspecific territorial interactions, and they are more generalized in their selection of prey, the habitat types they use, and their nest site requirements (Hamer et al. 1989). Their recent invasion into the range of the spotted owl (Taylor and Forsman 1976) is a possible source of competition between these closely related species. Evidence available already indicates that barred owls have displaced spotted owls from some sites in Washington (Hamer et al. 1989). Because barred owls have now been reported from about 27 different sites in California, interactions between these species will bear further study. A few hybrids between spotted and barred owls have been observed recently. Such hybridization is not uncommon between closely related species of wild birds. The extent of hybridization between these two owl species is still very limited, however, and the eventual outcome of this hybridization will take many decades or even centuries to resolve.

Diets

Spotted owls are "perch and pounce" predators (Forsman 1976), selecting an elevated perch from which they locate potential prey, either by sight or sound. When an owl detects a prey, it drops from its perch and attempts to capture the prey in its talons (the "pounce"). Spotted owls are agile, capturing prey in shrubs, trees, and on the ground. If a potential prey is in an inaccessible location or at some distance from the owl's perch, the owl may move closer before initiating its pounce. Its silent flight allows it to approach prey without being detected. In addition, spotted owls are adept at "hawking" behavior-capturing flying prey, primarily birds and insects.

Spotted owls forage primarily at night. Forsman et al. (1984) rarely observed daytime foraging by northern spotted owls, concluding that it occurred only opportunistically. On the other hand, Laymon (1991) concluded that California spotted owls in his study on the Eldorado NF, in the western Sierra Nevada, foraged regularly during the daytime when they were raising young, but not otherwise. Neal et al. (1989) reported that they often observed spotted owls-even nonbreeders-foraging for insects in the Sierra NF, taking them from bark surfaces, from

the ground, and even catching them in the air. These observations were usually in the late afternoon or early evening (Steger pers. comm.).

Marshall (1942) was the first to report on diets of the California spotted owl, based on stomach contents of two specimens and 23 regurgitated pellets gathered beneath roost trees at Whitaker Forest, Tulare County, in Sierran mixed-conifer forest with giant sequoias, at an elevation of about 5,500 feet in the western Sierra Nevada. The stomachs contained limb bones of frogs or toads, four bats (genus *Myotis*), one deer mouse, and four crickets ("probably *Gryllus*"). The pellets contained remains of 11 flying squirrels, two deer mice, and single individuals of four other mammal species, six bird species, and one June beetle. The relatively high proportions of flying squirrels and birds in this small sample are in line with several recent, more extensive studies of spotted owl diets in conifer forests of the Sierra Nevada (table 4A).

California spotted owls eat a variety of prey. For example, three samples from Sierran mixed-conifer forests produced a combined list of at least 78 different species—at least 1 amphibian, 1 lizard, 24 birds, at least 34 mammals, and at least 18 insects from a combined total of 2,716 prey items (Marshall 1942--63 prey items; Laymon 1988-1,275 prey items; Steger and Eberlein pers. comm.-1,405 prey items). In spite of this diversity, only one to five species or species-groups comprised at least 5 percent, by weight, of the owls' diets in the eight samples shown in table 4A, and at least 85 percent of the total biomass in each sample consisted of only one to four species or species-groups. Either northern flying squirrels or dusky-footed woodrats, or both, dominated prey biomass in all samples. Preliminary results from an analysis of the spotted owl's diet in the San Bernardino Mountains agree—about 80 percent of the biomass was dusky-footed woodrats, and about 10 percent consisted of medium-sized mammals like northern flying squirrels and gophers (Smith pers. comm.). The general pattern suggests a prey specialist with a search emphasis on just a few species, but which will capture and eat a wide variety of species and sizes of prey as they are encountered.

Four patterns in the results of these studies may be important: (1) Spotted owls in conifer forests of the Sierra Nevada, particularly above mid-elevation mixed-conifer forests (about 4,000-5,000 feet, depending on latitude), prey mainly on flying squirrels. (2) Owls in the mid- to lower elevations of the mixed-conifer zone and the upper part of the ponderosa pine/hardwood belt prey heavily on both flying squirrels and woodrats. (3) Both of these sets of owls consume a relatively high proportion of diurnal squirrels and/or birds, suggesting more daylight foraging than is the case for spotted owls elsewhere. And (4) spotted owls in the Sierran foothills and throughout southern California, even at high elevations, obtain 79 to 97 percent of their energy needs from woodrats. A dichotomy between flying squirrel and woodrat dominance of the diet is known for the northern spotted owl as well (review in Thomas et al. 1990, p. appendix J; Carey et al. 1992). Given the California spotted owl's diet, therefore, we need to consider ways to manage for habitats that will maintain thriving populations of flying squirrels in Sierran conifer forests and woodrats everywhere else.

Although woodrats dominate owl diets in Sierran foothill riparian/hardwoods and throughout the owl's range in southern California, only about 25 percent of all California spotted owl sites are in habitats where woodrats are abundant (table 1B). The remaining 75 percent occur in Sierran conifer forests where flying squirrels are the primary prey species.

Ecological Relations

Owls and Their Prey

Common sense tells us that no animal species can survive or reproduce in areas without sufficient food, but documenting these relations by direct field studies is usually very expensive and time-consuming. For owls in general, the time needed for such studies is typically several years, or even decades, depending on the life span of the owl species studied and the kinds of prey they eat. For example, owls with diets consisting mainly of small mammals whose populations exhibit regular, cyclic "booms" and "busts" in numbers, will require longer studies to cover at least two cycles of the prey. In spite of the high demands on time and resources to complete such studies, many have been reported in the literature on owls of the world. They portray a general picture of a marked dependency of owls on the availability of their key prey species—a fact widely recognized among raptor biologists in general and owl specialists in particular.

Relations between owls and prey are manifested in a variety of ways; some species of owls are affected in several ways. A moderately extensive (but not exhaustive) search of the world's literature on owls revealed at least five common, major effects of prey availability on owl biology (table 4B): Owl reproductive rates are often positively related to prey availability. Some species of owls nest earlier when and where prey are more abundant and available. Some owl pairs do not even attempt to nest when prey are scarce. The density of breeding owls is commonly higher when and where prey species are more abundant and available. And some species of owls exhibit major movements (whole populations may shift) when prey become scarce in the area occupied.

Several studies linking prey and spotted owls have been undertaken (Thomas et al. 1990), but little evidence has been found of relations between prey abundance and the biology of spotted owls. In a study in northwestern California, Ward (1990) found that prey abundance (mainly woodrats) was low and that it varied over the landscape. The owls did not necessarily forage in stands where woodrats were most abundant, but they hunted instead in areas where the availability of prey was more predictable. The strategy suggests one of optimizing search effort. Only the study of northern spotted owls in Washington and Oregon by Carey et al. (1992) has been intensive and extensive enough to suggest relations between the owls and their prey. Owls in

Table 4B—Review of ecological relations between owls and the relative availability of their prey. Researchers report a variety of relations, grouped here into five categories, from owl species in North America, Europe, and northern Asia.

Species	Observed ecological relations				
	Reproductive rate positively related to prey abundance	Earlier nesting when prey are abundant	Some pairs do not nest when prey are scarce	Breeding density higher when prey are abundant	Exhibit major movements when prey are scarce
Common barn-owl	Otteni et al. 1972 Baudvin 1975, 1976 Kaus 1977 Bunn et al. 1982 Colvin & Hegdal 1985				Bunn et al. 1982
Eagle owl			Olsson 1979		
Great horned owl	Houston 1971, 1975 Adamcik et al. 1978 Rusch et al. 1972	Adamcik et al. 1978	Houston 1971, 1975 Rusch et al. 1972	Rusch et al. 1972	
Snowy owl	Portenko 1972 Bunn et al. 1982 Mikkola 1983		Bunn et al. 1982	Bent 1938 Pitelka et al. 1955 Watson 1957 Parker 1974 Wiklund & Stigh 1986	Gross 1947 Mikkola 1983
Northern hawk owl	Mikkola 1983			Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985
Eurasian pygmy-owl	Sonerud et al. 1972 Jussila & Mikkola 1973 Kellomäki 1977 Solheim 1984				Mikkola 1983 Cramp 1985
Great gray owl	Mikkola 1983		Mikkola 1981, 1983		Green 1969 Nero 1980 Mikkola 1983
Tawny owl	Linkola & Myllymäki 1969 Southern 1970 Petty 1987		Southern 1970 Petty 1987	Mikkola 1983 Hirons 1985	
Ural owl	Lundberg 1976, 1981 Lundberg & Westman 1984 Pietäinen et al. 1986 Pietäinen 1988, 1989	Linkola & Myllymäki 1969 Lundberg 1981 Lundberg & Westman 1984 Pietäinen et al. 1986 Pietäinen 1988, 1989	Lundberg 1981 Lundberg & Westman 1984 Pietäinen 1988, 1989		
Long-eared owl	Hagen 1965 Linkola & Myllymäki 1969 Ziesemer 1973 Nord 1978 Mikkola 1983 Village 1985	Village 1985	Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985 Village 1985	Mikkola 1983
Short-eared owl	Rendall 1925 Mikkola 1983 Cramp 1985 Lockie 1955			Lockie 1955 Pitelka et al. 1955 Holzinger et al. 1973 Clark 1975 Mikkola 1983	
Boreal owl (Tengmalm's)	Linkola & Myllymäki 1969 Mikkola 1983	Mikkola 1983 Korpimäki 1987		Mikkola 1983	Mysterud 1970 Mikkola 1983 Korpimäki 1986

western hemlock forests on the Olympic Peninsula of Washington used about 4,200 acres of old forest annually; those in Douglas-fir forests in southwestern Oregon used about 2,000 acres of old forest annually; and owls in mixed-conifer forests in southwestern Oregon used about 1,120 acres of old forest annually. Estimates of the combined biomass of primary prey species taken by the owls were 5.3, 21.3, and 29.4 ounces/acre in the three forest types, respectively. Carey et al. (1992, p. 241) concluded that "Geographic variation in the areas traversed and amounts of old forest used by spotted owls reflected similar variation in the abundance and diversity of the medium-sized mammals that are the preferred prey of the owl."

Understanding Spotted Owl Habitats Through Ecological Linkages

A full understanding of why California spotted owls occur where they do, and why they do or do not reproduce well enough to maintain their populations, depends ultimately on comprehending how various components and functions within forest and woodland ecosystems relate to the owl's ecology. Here we have attempted to interpret some of those relations in terms of the owl's key prey species, typical nest sites, and the general dynamics of forest and woodland ecosystems where California owls are known to occur and reproduce. A general graphic representation of these relations helps to envision how all the

pieces fit together (fig. 4G). Assuming that presence and nesting by California spotted owls depends on the availability of a sufficient prey source, we believe that much of what is known about the owl's habitat associations can be better understood in relation to the ecology of its primary prey, especially northern flying squirrels and dusky-footed woodrats. Other key linkages relate to assuring an abundance of suitable nest sites. How does all of this relate to what we judge to be important attributes of suitable owl habitat?

Why Big, Old Trees?

Large, old trees are preferentially selected for nest sites by spotted owls (Chapter 5). For example, nest trees averaged larger than 40 inches in d.b.h.—much larger than the mean diameter of trees generally available. About one fifth of all nests found were in snags (dead trees) and about four fifths were in live trees. Two thirds of the nests were in large, natural cavities formed by decay at sites where branches broke off or tore out of the trunk of the tree, and another 20 percent were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions typically develop only after a tree is relatively old. In addition, larger trees are needed to provide large snags and longer-lasting components of dead, decaying wood on the ground, especially in the form of large logs but also in fallen limbs of various sizes.

Why Downed Woody Debris?

Functional linkages among spotted owls, their major prey species, the prey's food, and the general forest or woodland/shrub community where these linkages occur can be traced in figure 4G. Some major linkages are highlighted by broader arrows. For example, northern flying squirrels feed extensively on hypogeous (underground) fungi, especially during periods when the ground is not covered by snow. They may even cache some of these fungi to be eaten after snowfall. At least two California studies (McKeever 1960, Hall 1991) and one Oregon study (Maser et al. 1985) found that flying squirrels eat primarily fungi and lichens. Hypogeous fungi comprised the bulk of the summer diet, and the winter diet was largely arboreal lichens. The density of flying squirrels in red fir/white fir stands in the Lassen NF was strongly associated with the abundance of truffles (fruiting bodies of hypogeous fungi), and truffle abundance was strongly associated with the presence of a well-developed soil organic layer and a large volume of decaying logs (Waters and Zabel 1992). These data suggest that management practices that decrease the soil organic layer and the number of large, decaying logs will reduce the capability of a habitat to support flying squirrels, and possibly spotted owls as well.

Hypogeous fungi probably also comprise a major food source for white-footed mice (Maser et al. 1978a), an important prey species of the California spotted owl. Spores of the fungi pass unharmed through the digestive tract of these and other small mammals that consume them and are thus spread in fecal pellets over the forest floor. All hypogeous fungi are also mycorrhizal: "Mycorrhiza literally means 'fungus-root' and denotes a symbiotic relationship between certain fungi and plant roots" (Maser et al. 1978b, p. 79). Trees depend on mycorrhizae for an

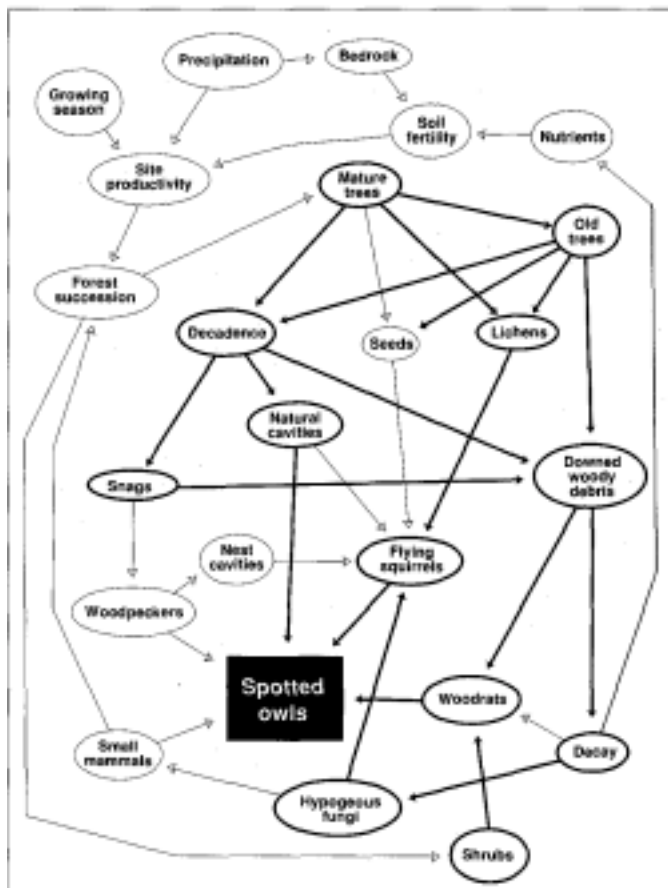


Figure 4G—Simplified, schematic representation of some important ecological linkages associated with California spotted owls.

adequate uptake of various nutrients, and the fungi benefit by obtaining carbohydrates produced by the trees. Interestingly, the spores of hypogeous fungi are spread by the small mammals that eat them, thus completing a loop of interdependencies in forest ecosystems (fig. 4G).

As important as large, decaying logs are to functional ecosystems where spotted owls seem to thrive, logs that are positioned perpendicular to the slope of the land are most valuable. This is because they are best situated to intercept soil and water moving downslope and, as a result, to become a substantial water reservoir as they reach an advanced state of decay. Even more important is the fact that very large logs can make a vital contribution to the forest ecosystem for a longer period than they did as standing, live trees (Maser 1989). These log reservoirs provide refuges for many animal species during hot, dry parts of the year, just as they provide water to trees whose roots, aided by the symbiotic fungal mycorrhizae, have penetrated them. To ignore the role of logs in our forest ecosystems may be to lose those ecosystems in the long run.

Why Snags?

Spotted owls occasionally select snags for nest sites, either on their broken top or in natural cavities in the snags, cavities that either carried over from the live tree or were created by decay after the tree died. Among the 263 nests reported in our sample from conifer forests (table 5I), 17 percent were in snags. Snags provide the primary nesting substrate for many other cavity-nesting birds as well. Woodpeckers, which are occasionally captured and eaten by spotted owls (table 4A), excavate nesting and roosting cavities, and a variety of nonexcavating species later use the same cavities for nests or roosts. Of particular significance in the ecology of spotted owls, flying squirrels often use old woodpecker cavities for den sites. Finally, snags eventually fall and contribute to the accumulation of decaying wood on the ground. Therefore, the snag component benefits the owls both directly and indirectly in a variety of ways (trace arrows in fig. 4G).

Why Multiple Canopy Layers?

A possible ecological explanation for the prevalence of multi-layered canopies in habitats frequented by spotted owls is not clear. The structural diversity associated with these "layers" may contribute to a greater diversity of prey species. Perhaps, as Barrows and Barrows (1978) have hypothesized, the different layers provide opportunities for the owls to move up and down within the overall canopy to find the most comfortable microclimate for roosting. Or they may be important in allowing foraging owls to use perches at a variety of heights as they search for prey. On the other hand, multiple layers may be simply a covariate of some other component of the owl's habitat that is vital, such as the owl's prey.

Why Dense Canopies?

Among the most consistent habitat relations found for spotted owls is their greater use than expected of stands having 40 percent or greater (foraging) and 70 percent or greater (nesting and roosting) total canopy cover (Chapters 5 and 6). Like the owl's association with multiple canopy layers, however, possible reasons for this are not readily apparent. It may relate to one

or more of the following: (1) Denser stands tend to be cooler and, as proposed by Barrows (1981), they would allow the owls a wider range of choices for locating thermally comfortable roosts. (2) Denser stands provide more concealing cover, where the owls may be able to nest and roost with less chance of discovery by potential predators. It may be no coincidence that their plumage is speckled, as this pattern would tend to camouflage them during the daytime in a forest full of sunflecks. (3) In conifer forests, where flying squirrels dominate the owls' diet, prey may be more abundant and available in denser forest stands (see Chapter 10). This would not necessarily account for the same observed relation between canopy cover and owl habitat use in areas where woodrats dominate the diet, however, because woodrats tend to be most abundant in relatively dense stands of shrubs. To benefit owls, these must be intermingled with, or adjacent to, the hardwood stands where the owls roost and nest.

Why Differences in Home-Range Size?

In general, the largest home ranges of California spotted owls occur where flying squirrels comprise the majority of the owl's diet and the smallest home ranges occur where woodrats dominate. Home ranges of spotted owls in conifer forests of the Sierra NF are several times larger than home ranges <10 airline miles away, in foothill riparian/hardwood forests (Neat et al. 1990). Owls in the conifer forest prey mainly on flying squirrels, but those in the low-elevation hardwood stands prey almost exclusively on woodrats (table 4A).

The importance of these prey to the ecology of spotted owls has been emphasized by the bolder connecting links in figure 4G. Although only one study of spotted owls has shown a clear connection between prey abundance and areas used by the owls (Carey et al. 1992), we strongly suspect that the approximately 10-fold difference in observed home-range sizes of California spotted owls results primarily from regional differences in diet. Apart from common sense and the study by Carey et al., our strongest scientific support for this contention is the degree to which densities and reproductive activities of owl species throughout the world—at least those that have been studied well enough to establish the relations—are influenced by the availability of their prey (table 4B). Not only are woodrat populations denser than flying squirrel populations, often by at least 10-fold (Chapter 10), but also woodrats weigh nearly twice as much as flying squirrels.

Why Do Most Pairs of Owls Not Nest Every Year?

Spotted owls exhibit marked yearly variation in the proportion of pairs that nest. This has ranged from essentially no pairs to nearly all pairs nesting. For example, from as low as 11 percent to as high as 70 percent of owl pairs in the Eldorado demographic study have nested in different years (R. J. Gutiérrez, pers. observ.). On the other hand, Franklin et al. (1990) reported little variation in the proportions of pairs nesting during a 6-year study in northwestern California. Much annual variation has also been observed in nesting success (proportion of pairs nesting that also fledge young) from year to year and from region to region, ranging from as low as 0 to as high as 100 percent (Forsman et al. 1984, Gutiérrez et al. 1984, Thomas et al. 1990, Lutz 1992, LaHaye et al. 1992).

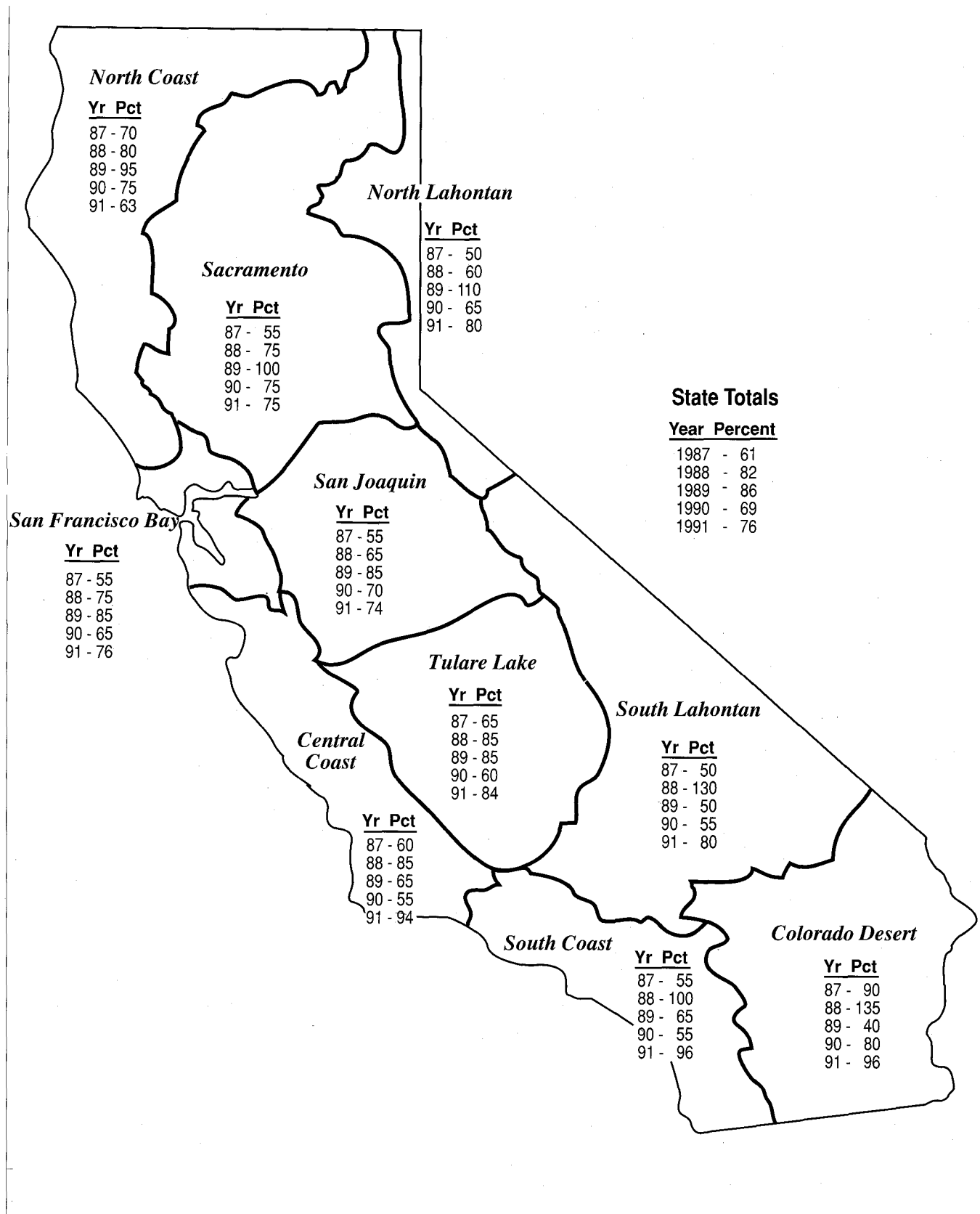


Figure 4H-Percentages of mean annual precipitation in California from 1987 through 1991, by water year (1 October through 30 September) and hydrologic region (California Department of Water Resources 1991).

Surveys of California spotted owls have been used to determine distribution, density, and other measures of "status" (see tables 3A, 3B, 3F, and 3H-J). These counts overestimate the functional owl population, however, because pairs do not occupy all sites in all years, occupied sites do not always support pairs, and each pair does not breed every year. A compilation of results from sites occupied for 4 consecutive years, adjusted to represent 50 known sites where owls defended a territory in any one of the 4 years (G. I. Gould, Jr., pers. observ.), suggests that only about 41 sites would be occupied in a given year, 34 would be occupied by pairs, and only 11 of those would produce young. Over the 4-year period, owls at 20 sites, usually the most consistently occupied, would produce 90 percent of the young.

For many owl species, failure to breed in some years has been shown to result from low prey availability (table 4B). As for home-range size, even lacking definitive studies of spotted owls, we strongly suspect that the local prey base largely determines whether a given pair of owls attempts to nest in a given year, and whether it succeeds if it does make an attempt. Drought may be a corollary here. Nearly all of the detailed studies of the California spotted owl, upon which this report is based, have been done during an ongoing drought that began in 1987 (fig. 4H). A variety of scenarios might occur. For example, drought has been observed to depress woodrat populations or not to affect them (Chapter 10), so the drought may or may not have lowered reproduction among the owls. Mild winters accompanying the drought may have increased the survival rates of the owls or the flying squirrels, or both. We cannot reach conclusions about these or other options. All we can do is acknowledge the attendant uncertainty.

Conclusions

California spotted owls share many attributes of their natural history with the northern spotted owl. Yet our knowledge of the California spotted owl's biology is meager relative to its more famous northern relative. For example, we are not yet able to set clear bounds on the range of habitats that are capable of supporting self-sustaining populations of the California subspecies (Chapter 8). And we are not likely to be able to do this until the owls have been studied thoroughly during both wet and dry climatic cycles. Our only good estimate of juvenile survival rate for the subspecies is based on the population in the San Bernardino Mountains (Chapter 8), although we estimate that about 75 percent of all California spotted owl pairs occur in the Sierra Nevada, where habitat change (by logging) is of greatest concern. Similarly, with the exception of the San Bernardino Mountain study, estimates of age-class survival and fecundity schedules are lacking or are imprecise. No studies are available that relate California spotted owl populations to populations of their prey species. Finally, we know little about the factors important

in the biology of the owl's primary prey species. The work of Waters and Zabel (1992) on flying squirrels in the Lassen NF is exemplary in that regard. Their work needs to be replicated elsewhere, and equally comprehensive studies of woodrat ecology need to be undertaken.

The general lack of information about nearly all phases of the California spotted owl's biology and ecological relations leads to high uncertainty about its present status. Because of this uncertainty, we recommend continuation of basic ecological studies and prudent forest management-following practices that will maintain future options.

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